ARKIV FÖR BOTANIK.
BAND 19. N:o 2.

Die höhere Wasservegetation des Bach- und Teichgebietes bei Aneboda.

Von

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Mit 10 Tafeln und 2 Figuren im Texte.

Mitgeteilt am 10. Oktober 1923 durch O. NORDSTEDT und S. MURBECK.

Seit der Einrichtung des ersten limnologischen Laboratoriums in Schweden bei Aneboda in der Provinz Småland im Jahre 1907 sind dort eine Reihe von Untersuchungen ausgeführt worden, welche sich auf die verschiedensten Verhältnisse der früher fast vollständig unbekannten Limnologie der oligotrophen Gewässertypen beziehen.

Es liegt wohl in der Natur der Sache, dass diese Untersuchungen von Anfang an zum grossen Teil auf die Plankton- und Bodenverhältnisse der Seen und Teiche gerichtet waren. Denn hier waren von Anfang an die entsprechenden Verhältnisse der eutrophen Gebiete einigermassen bekannt und es bestand deshalb auch die Möglichkeit, durch ein genaueres Studium derselben unter oligotrophen Bedingungen eine vergleichende Limnologie auf dem Gebiet der Plankton- und Bodenkunde begründen zu können. Die Entwicklung der Limnologie in den letzten Jahren dürfte auch das Berechtigte in dieser Auffassung nunmehr vollauf gezeigt haben.

Verschiedenen Zügen in dem allgemeinen Produktionsbild der oligotrophen Gewässer wurde aber hierbei vorläufig nur mehr nebensächliche Aufmerksamkeit gewidmet. In erster Linie tritt dies für die gesamte höhere Vegetation der oligotrophen Gewässertypen zu.

Das Studium der höheren Wasservegetation ist überhaupt von der pflanzensoziologischen Forschung noch sehr wenig be-

trieben. Sogar die einfachsten Prinzipienfragen sind noch nicht von diesem Gesichtspunkt aus in unserem Land behandelt. Dass unter derartigen Voraussetzungen diesbezügliche Arbeiten, welche auch den Anforderungen der jetzigen Limnologie genügen sollen, mit den grössten Schwierigkeiten zu tun haben, liegt ja ohne weiteres auf der Hand.

Vor einigen Jahren begann ich aber nichts desto weniger die Zonationsverhältnisse in den oligotrophen Seentypen der Aneboda-Gegend etwas eingehender zu studieren. Um dabei auch eine allgemeine Übersicht über die Wasservegetationsverhältnisse des Gebietes überhaupt an der Hand zu haben, wurde auch eine Untersuchung der gesamten Wassersysteme bei Aneboda vorgenommen.

Von den Ergebnissen dieser Untersuchung soll aber im folgenden nur eine kurzgefasste Übersicht der Vegetationsverhältnisse des Bach- und Teichsystems bei Aneboda mitgeteilt werden.

Diese Aufgabe gehört, wie ich sie hier gefasst habe, zu den einfacheren. Aus drei Gründen glaube ich aber, dass sich eine Publikation dieser Ergebnisse als nützlich erweisen wird.

Erstens sind die Vegetationsverhältnisse unter oligotrophen Verhältnissen in Bächen und periodischen Teichen unseres Landes früher niemals Gegenstand einer näheren Untersuchung gewesen. Zweitens wird diese Abhandlung zeigen, wie die Verhältnisse sich zuerst in neuen ablassbaren Teicharealen relativ ungestört bis auf den jetzigen Standpunkt entwickelt haben. Eine diesbezügliche Schilderung hat dadurch schon an und für sich ihren Wert, noch mehr aber als Ausgangspunkt künftiger teichwirtschaftlicher Vegetationsstudien. Da nämlich die Vegetationsverhältnisse teichwirtschaftlich eine grosse Rolle spielen können, so ist diese Frage zum grossen Teil auch von rein praktischem Interesse. Wahrscheinlich wird auch die teichwirtschaftliche Praxis der Zukunft tiefer in die natürlichen Verhältnisse eingreifen und somit vielleicht die jetzigen Verhältnisse völlig verändern. Drittens wünschte ich auch mit dieser Darstellung einen Grund für andere Untersuchungen, welche in einer oder anderer Hinsicht von den Vegetationsverhältnissen abhängig sind, zu legen.

Meine Vegetationsstudien bei Aneboda sind durch eine reichliche Subvention aus der C. F. Lundström'schen Stiftung besonders gefördert worden. Es ist mir eine angenehme Pflicht dies hier mit grösster Dankbarkeit anzuerkennen.

I. Die Wassersysteme Anebodas.

Das Aneboda-Gebiet gehört den kalkärmsten Urgebirgsgegenden (Granit- und Gneisformation) der Provinz Småland an. Geographische Lage etwa 57° 8′ n. Br. Höhe über dem Meer etwa 200 m. Jährliche Mitteltemperatur + 5 à 6° C., für Januar — 2 à 3° C., für Juli + 16° C. Jährliche Niederschlagsmenge 500 à 600 mm.; für Juli etwa 90 à 100 mm.; für Oktober 60 à 70 mm. Waldvegetation von dem Haupttypus der südschwedischen Nadelwälder. — Näheres hierüber bei E. NAUMANN, 1917.

Die Hauptcharaktere der Wasserchemie sind die folgenden: Oligotypus von Ca, P und N; Oligo- bis Polytypus von Humus. Es ist somit in dem Gebiet nur mit folgenden Gewässertypen zu rechnen: Der oligotrophe Typus in seiner orthotrophen bezw. paratrophen Ausbildung. (Vergl. E. NAUMANN 1921, b.) Eine ausführlichere Darstellung der chemischen Wasser- und Bodenbeschaffenheit in dem Teichgebiet Anebodas habe ich in meiner Abhandlung über die Phytoplanktologie der Teiche (1924), auf die ich in dieser Hinsicht hinweise, gegeben.

Die topographischen Verhältnisse der Aneboda-Gegend sind aus der umstehenden Karte ohne weiteres ersichtlich.

Zu dem Wassersystem des humusmesotrophen Sees Stråken gehören die folgenden Seen:

1. Der See Fiolen (humus-oligotroph).

Das Wasser fliesst durch den Fiolenbach zuerst gegen O, dann überwiegend gegen N. Mündet in den Stråkensee durch zwei Arme, von welchen der südlichste nunmehr nur periodisch fliesst.

Dieser Bach speist das Hauptgebiet der Teichanstalt bei Aneboda. Das ursprünglich humusoligotrophe Wasser wird durch die Passage durch das Hochmoor bei Åkhult, bezw. durch die Stauung über den Moorböden des Teichgebietes humusmeso- bis humuspolytroph.

2. Der Förhult-See (humus-mesotroph).

Der Förhult-Bach vereinigt sich bald mit dem Skärsmo-Bach.

3. Die Skärsmo-Seen (humus-mesotroph).

Der entwässernde Bach vereinigt sich bald mit dem Förhult-Bach. Dieser Eskås-Bach fliesst später mit dem nördlichen Arm des Fiolen-Bachs zusammen, und der hieraus entstandene Aneboda-Bach ergiesst sich dann in den See Stråken. Der Eskås-Bach speist ein Nebengebiet der Teichanstalt bei Aneboda.

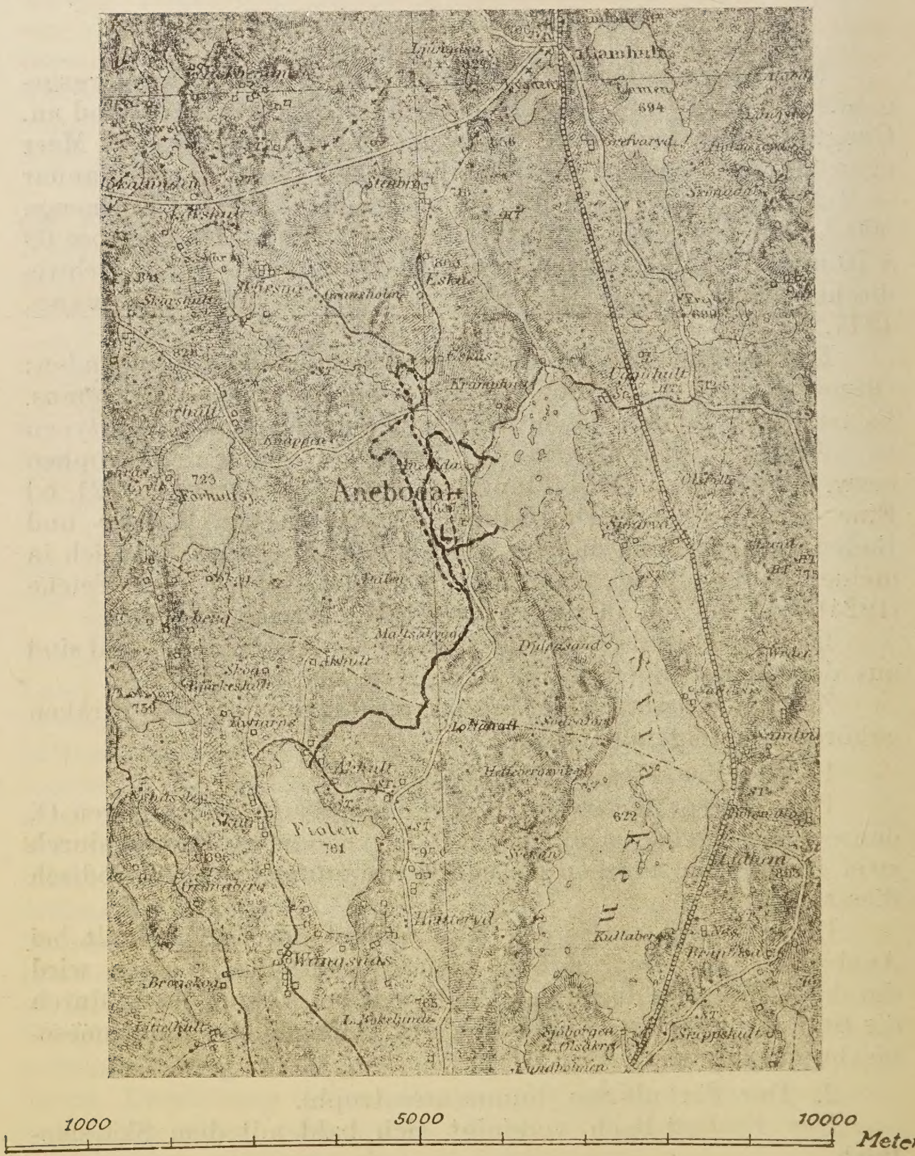

Fig. 1. Übersichtskarte über das Bach- und Teichsystem bei Aneboda.

Die ungefähre Begrenzung des Haupt- und Nebengebietes der Teichanstalt ist gestrichelt.

L = Lage des limnologischen Laboratoriums.

[Strombahn des Fiolen-Baches besonders markiert.]

Von diesen verschiedenen Gewässern werden wir im folgenden vor allem den Fiolen-Bach als einen Typus der oligotrophen Urgebirgsbäche ebenso wie das Teichgebiet in seiner Gesamtheit etwas näher besprechen.

II. Die Artenliste.

Die vorliegende Untersuchung wird auf die eigentlichen höheren Wassergewächse streng begrenzt.

Die Artenanzahl ist hier eine sehr geringe. Über ihre Qualität und ihr Vorkommen orientiert näher die umstehende tabellarische Übersicht, S. 6—7.

Die Bestände, welche von den hier verzeichneten Pflanzen aufgebaut werden, zeichnen sich bekanntlich im allgemeinen durch eine oft auffallende Reinheit aus.

Mit Rücksicht hierauf habe ich für den Zweck der vorliegenden Untersuchung auf jede nähere Bestandsanalyse verzichtet. Das beigegebene photographische Bildermaterial, das von mir selbst in den Jahren 1916—1923 aufgenommen ist und auf dessen zweckmässige Herstellung besonders geachtet wurde, dürfte auch in dieser Hinsicht besser als Worte sprechen. Allerdings konnte nur eine sehr kleine Auswahl aus diesem Material in der vorliegenden Publikation aufgenommen werden.

Es wird die Hauptaufgabe der vorliegenden Untersuchung sein, festzustellen, wie sich die Arten in dem Gebiet z. Z. verbreitet haben; einige von den auffallenderen Ursachen hierfür sollen näher klargelegt werden. Daran schliesst sich noch eine Besprechung der Teichvegetation in teichwirtschaftlicher Hinsicht.

III. Die Bachflora.

A. Der Fiolen-Bach.

(Vergl. Tafel I—V.)

Der Lauf des Fiolen-Bachs ist schon zum wesentlichen Teil erheblich reguliert. Allerdings sind noch einige Strecken in ihrem Naturzustand zurückgeblieben.

Folgen wir also zuerst dem Fiolen-Bach vom Fiolen-See bis zu seiner Einmündung in den Aneboda-Bach. Es ergeben sich dann im grossen und ganzen folgende Abschnitte.

Tab. I. *Artenliste der höheren Wasservegetation des Bach- und Teichgebiets bei Aneboda.*

Art	Verbreitung in den Seen	Verbreitung in den Bächen	Verbreitung in den Teichen
Acorus calamus	—	Nur im Mühlenteich des Aneboda-Baches.	—
Alisma Plantago aquatica	—	Im Fiolen-Bach bei den Stenfälle-Teichen. — Im Skärsmo-Bach, vereinzelt.	Nur in einigen Teichen im Hauptgebiet der Teichanstalt.
Calla palustris	+	Ziemlich allgemein.	Ziemlich allgemein.
Callitriche hamulata	+	» »	» »
» *stagnalis*	+	» »	» »
Carex rostrata	+	Sehr allgemein.	Sehr allgemein.
» *Hudsonii*	+	Selten.	Selten.
Equisetum limosum	+	Ziemlich allgemein.	Ziemlich allgemein.
Glyceria fluitans	+	Sehr allgemein.	Sehr allgemein.
Juncus supinus f. *fluitans*	+	» »	Selten.
Lemna minor	—	—	Selten, nur im Hauptgebiet.
Lobelia dortmanna	+	Selten. Allerdings vorhanden unmittelbar oberhalb sowohl des Haupt- wie des Nebengebiets der Teichanstalt.	In einem Teich des Nebengebiets. Nicht in den Teichen des Hauptgebiets.
Menyanthes trifoliata	+	Ziemlich allgemein.	Selten.
Myriophyllum alterniflorum	+	Selten.	—
Naumburgia thyrsiflora	+	Ziemlich allgemein.	Ziemlich allgemein.
Nuphar luteum	+	» »	Selten.

Nymphæa alba	+	Nicht im Fiolen-Bach. Sonst ziemlich allgemein.	Nicht im Hauptgebiet. Im Nebengebiet vorhanden, zerstreut.
Potamogeton alpinus	—	—	Nur in einigen Teichen des Hauptgebiets.
» *natans*	+	—	Sehr allgemein verbreitet.
» *polygonifolius*	—	Sehr allgemein verbreitet.	—
» *pusillus*	+	—	Selten.
Phragmites communis	+	Nur im Fiolen-Bach, selten.	—
Scirpus lacustris	+	Nur im Eskås-Bach, selten.	Nur in einem Teich des Hauptgebiets.
» *palustris*	+	Allgemein.	Allgemein.
Sparganium ramosum	—	Selten.	Selten.
» *simplex*	—	Ziemlich allgemein.	Ziemlich allgemein.
Typha latifolia	Nur in dem See S. Skärsmosjön	—	Nur in einem Teich des Haupt- und in einem Teich des Nebengebiets.
Utricularia minor	+	+	Ziemlich allgemein.
Amblystegium Kneiffii (Det. S. MEDELIUS)	?	?	Massenhaft in einigen Teichen des Hauptgebiets.
» *exannulatum* (Det. S. MEDELIUS)	?	?	
Fontinalis dalecarlica	?	Ziemlich allgemein.	—
Isoëtes lacustre	+	Nur im Mühlenteich bei Eskås.	—

\+ Vorhanden.
— Nicht vorhanden.

1. Der Lauf bei Åkhult.

(Vergl. Tafel I.)

Nach dem in den letzten Jahren kanalisierten Auslauf aus dem Fiolen-See (Kraftwerk!) zieht der Bach durch die Randzone des grossen Hochmoors bei Åkhult. Auch dieser Abschnitt ist dann und wann — und zwar aus landwirtschaftlichen Gründen — ausgegraben worden.

Die Breite des Baches ist hier nur etwa 2 m. Stromgeschwindigheit des normalen Sommerwassers im vegetationsarmen Mittelauf = 10 m./Min., im vegetationsreicheren = 1 m./Min. Tiefe des Mittellaufes = ca. $^1/_2$ m.

Als Bestandbildner machen sich hier nur die folgenden Pflanzen geltend: *Carex rostrata*, *Glyceria fluitans*, *Juncus supinus f. fluitans*, *Myriophyllum alterniflorum*, *Potamogeton polygonifolius*, *Sparganium ramosum*, *S. simplex*. In nur vereinzelten Exemplaren treten auf: *Equisetum limosum*, *Nuphar luteum*. — In negativ charakterisierender Hinsicht ist besonders das Fehlen von *Phragmites* und *Scirpus* zu bemerken.

Von den angeführten Beständen tritt der aus *Juncus supinus* f. *fluitans* bestehende am häufigsten auf. Er beherrscht oft den ganzen Mittellauf. Viel seltener findet man hier die *Myriophyllum*- bezw. die *Potomogeton polygonifolius*-Bestände.

Die Bestände von *Carex rostrata* und von *Sparganien* treten typisch nur an den Seiten des Laufs und zwar nur in geringerer Schwung auf. Eine Besiedelung des Mittellaufes durch diese Pflanzen scheint an und für sich hier ausgeschlossen. In den Fällen aber, wo die Stromgeschwindigkeit durch die in der Mitte des Laufes wuchernde *Juncus supinus* f. *fluitans*-Bestände ganz erheblich herabgesetzt wird, tritt hie und da eine derartige Besiedelung sekundär auf.

Im Vergleich zu den genannten Beständen der emersen Formation spielen die *Glyceria*-Bestände eine grössere Rolle. Sie können auch ohne weiteres sogar den Mittellauf kolonisieren und demnach durch Stauungen eine Auswanderung der oben genannten Randpartie-Bestände nach dem Mittelauf ermöglichen.

Fast der gesamte Lauf bei Åkhult wird durch einen sehr einseitig einwirkenden Faktor gekennzeichnet: die Eisen-Polytrophie. Durch die Wirksamkeit des im Randgebiet des Åkhultmoors hervortretenden eisenhaltigen Grundwassers ist der Boden des Bachlaufes mit losem Ocker überschichtet. Die ganze Vegetation ist weiter vollständig mit Eisenocker beladen. Von der submersen ist oft nichts anderes als die wogenden

Ockermassen zu bemerken. Betreffs der Entstehungsweise derartiger Ockerablagerungen sei hier nur auf meine diesbezügliche Abhandlung l. c. 1921 a hingewiesen. In ökologischer Hinsicht mag hier auch die Bemerkung genügen, dass dieser Überfluss an Eisen die Standortsbedingungen für die Flora doch sichtlich nicht in absehbarer Weise beeinflusst. Anderorts im Lauf finden wir nämlich fast dieselbe Flora bei Abwesenheit der Ockerablagerungen entwickelt.

Eine Reihe von für diesen Abschnitt charakteristichen Vegetationsbildern sind auf Tafel I zusammengestellt. Die Bilder sind alle im Herbste 1921 aufgenommen.

Fig. 1. Ein charakteristisches Bild eines neue ausgegrabenen Abschnittes. Jede Randvegetation fehlt. Centralvegetation schwach entwickelt, nur aus *Potamogeton polygonifolius* bestehend.

Fig. 2. Laufabschnitt bei einer weiteren Entwicklung der Besiedelung. Grosse Randvegetation, vor allem aus *Carex rostrata* bestehend.

Fig. 3. Laufabschnitt bei einer zentralwärts von den Randabschnitten aus fortschreitenden sekundären Besiedelung durch *Glyceria fluitans.*

Fig. 4. Laufabschnitt bei einer sehr weit fortgeschrittenen sekundären Besiedelung. *Carex rostrata* wandert hier über die aus *Potamogeton polygonifolius* gebildete Staudecke ins Zentrum des Bachlaufes ein.

2. Der Lauf bei Loftahall.

(Vergl. Tafel II.)

Bei Loftahall verlässt der Bach das eigentliche Hochmoor. Die Einwirkung des Eisengehaltes ist schon abgeklungen.

In jenem Gebiet kultivierter Moorflächen tritt indessen eine neue Eisenanreicherung auf. Sie klingt aber recht bald wieder ab.

Der Lauf ist hier breiter, das Wasser aber seichter, höchstens einige dm. tief.

Die Vegetation ist hier qualitativ viel spärlicher entwickelt. Die Bestände sind aber z. T. ziemlich dicht. Als Assoziationsbildner scheiden aus: die *Sparganía.* Als neue treten hinzu: *Callitriche hamulata*, *C. stagnalis*, *Phragmites communis.* Das übrige unverändert. Charakteristisch sind vor allem die stellenweise ziemlich dichten Bestände aus *Phragmites.*

Auch diese Flora wächst z. T. in einer ausgesprochenen Ockerablagerung. Der Eisengehalt klingt aber hier bald ab, etwa dort, wo der Bach das Loftahall-Gebiet verlässt.

Ein charakteristisches, im Herbst 1921 aufgenommen Vegetationsbild dieses Laufabschnittes ist auf Tafel II mitgeteilt.

Fig. 5. Lauf des Baches durch die Moorkulturen bei Loftahall. Die stellenweise Dichte der *Phragmites*-Bestände ist auffallend.

3. Der Lauf zwischen Loftahall und Bygget.

(Vergl. Tafel II—III.)

Der Bach verlässt das Kulturmoor bei Loftahall und zieht durch einen sterilen, gebüschüberbrückten, anfangs künstlich kanalisierten Lauf weiter.

Dieser Abschnitt des Bachlaufes befindet sich noch — vom Anfang abgesehen — im Naturzustand.

Der Lauf wird auf dieser Strecke durch 3 Fälle erheblich gesenkt. Die Fälle verlaufen über Steine und Felsen in einer teilweise sogar vollständig unberührten aber auch ziemlich unzugänglichen Landschaft. Zwischen den Fällen findet man kleinere Niederungen mit einer reichlichen Vegetation aus vor allem *Carex rostrata* und *C. Hudsonii*, wo der Bach in langsamem Serpentinlauf fliesst.

Die Fälle sind fast vollständig vegetationslos. Nur *Fontinalis* bildet hie und da kleinere Bestände auf den Steinen.

In dem Serpentinlauf machen sich als Bestandbildner die folgenden Arten geltend: *Calla palustris*, *Carex rostrata*, *Glyceria fluitans*, *Juncus supinus* f. *fluitans*, *Menyanthes trifoliata*, *Potamogeton polygonifolius*. Nicht vorhanden: Die *Sparganía*, *Phragmites*. — Auf Grusboden unterhalb des Falles bei Bygget findet man einen kleinen Bestand aus *Lobelia dortmanna*.

In vereinzelten Exemplaren — also nicht bestandbildend — findet man hier: *Equisetum limosum*, *Nuphar luteum*.

Von den hier angeführten Bestandbildnern sind *Calla* und *Menyanthes* ausgeprägte Randformen. Betreffs der Besiedelung des Mittellaufes sei auf das schon oben S. 8, 9 angeführte hingewiesen.

Sowohl *Calla* wie auch *Menyanthes* sind in erster Linie als Charakterpflanzen mehr oder weniger teichartiger Gewässer anzuführen. Wo teichartige Ausbuchtungen der Bachläufe jedenfalls periodisch auftreten, trifft man sie deshalb auch. Sie senden dann auch im Sommer einige Rhizome gegen das freie Wasser hin und können dann bei extrem geringem Wasserstand sogar den Lauf vollständig füllen.

Es ist unter diesen Voraussetzungen sehr wohl erklärlich, dass wir diese Pflanzen als Bestandbildner in dem Serpentinlauf finden, sie aber in dem tiefkanalisierten Hochmoorlauf vermissen.

Einige charakteristische Bilder dieses Abschnittes des Bachlaufes sind auf Tafel II—III zusammengestellt. Sie sind in den Jahren 1919—1921 aufgenommen.

Fig. 6. Der Bach verlässt den natürlichen Stauteich bei Bygget. — Man sieht hie und da im zentralen Lauf kleine Inseln von *Carex rostrata*, welche auf den von *Glyceria fluitans* gebildeten Staudämmen entstanden sind.

Fig. 7—8. Von dem reissenden Lauf in der Mitte des Bygge-Falles. Randvegetation nur in ruhigen, steinumbrückten Ecken durch *Naumburgia thyrsiflora.*

Fig. 9. Ein öder Gesteinsabschnitt im Fall. Fast keine Vegetation. Nur hie und da etwas *Naumburgia* bezw. *Potamogeton polygonifolius.* Auf den Steinblöcken Wassermoos, *Fontinalis dalecarlica.*

Fig. 10. Ruhiger Serpentinlauf unterhalb des Falles bei Bygget. Hauptvegetation: *Potamogeton polygonifolius.* Randkolonisation in erster Linie durch *Carex rostrata* und *Glyceria fluitans.*

Fig. 11. Detailbild des Serpentinlaufs. Links ein kleines Quellmoor. — Auswanderung von *Menyanthes* in den Mittlauf.

Fig. 12. Detailbild der Bachvegetation. Besiedelung des Mittellaufes durch *Carex rostrata* und *Menyanthes,* auf den primären Stauinseln von *Potamogeton polygonifolius* einwandernd.

4. Der Lauf unmittelbar oberhalb der Teichanstalt.

(Vergl. Tafel IV.)

Der Bach fliesst hier ziemlich geschwind in einem bis 3 m breiten Lauf über reingespülte Steine und Gerölle.

Die Vegetation ist hier sehr spärlich, d. h. die Bestände sind von einer sehr geringen Ausdehnung.

Im Mittellauf treten als Bestandbildner nur *Juncus supinus* f. *fluitans* und *Potamogeton polygonifolius* auf.

Wo aber die Stromgeschwindigkeit herabgesetzt wird, sei es durch die natürliche Topographie des Bachlaufes oder auch durch Driftanhäufungen bezw. durch primäre Ausdehnung der rheophilen Flora, dort treten noch einige andere Bestandbildner hinzu. Es sind dies die folgenden: *Carex rostrata, Glyceria fluitans, Naumburgia thyrsiflora.* Vor allem spielen hier durch Driftmaterial aus Waldabfall gebildete Staudämme eine grosse Rolle für die Besiedelung des Mittellaufes.

Einige für diesen Abschnitt charakteristische Bilder, alle im Herbst 1919—1921 aufgenommen, sind auf Tafel IV zusammengestellt.

Fig. 13. Abschnitt eines charakteristischen Stein- und Geröllaufes. Keine andere Vegetation als *Potamogeton polygonifolius* bezw. — in von dem Steinmaterial gebildeten, etwas ruhigeren Ecken — *Glyceria fluitans.*

Fig. 14. Staudämme aus Waldabfall in dem Stein- und Geröllauf unmittelbar oberhalb der Teichanstalt. Hierdurch Besiedelung durch *Carex rostrata*, *Glyceria fluitans* und *Naumburgia* im Mittellauf.

Schon an der Grenze der Teichanstalt gliedert der Bach einen Ast ab, der direkt an den Stråken-See geht. Die von der Teichanstalt durchgeführte Regulierung hat aber diesen Ast in einen nur periodisch — bei Hochwasser und bei Ablassung — laufenden Bach verändert.

Der Lauf dieses periodischen Baches geht z. T. durch ebenen Waldboden z. T. über Geröll. Die Hauptvegetation besteht aus *Glyceria fluitans*, *Potamogeton polygonifolius* und *Fontinalis dalecarlica.* Vor allem *Potamogeton polygonifolius* kann als für diesen periodischen Lauf sehr charakteristisch gelten. Sie kommt hier in einer überaus grossen Formenentfaltung vor, und zwar sowohl als Landpflanze in dem überwiegenden Teil des Laufes wie auch als Wasserpflanze in derartigen Abschnitten, wo Wasser auch in den trockensten Sommern vorhanden ist.

5. Der Lauf durch die Teichanstalt.

(Vergl. Tafel IV—V.)

Der Bach stürzt bei dem Teich Övre Hållsdammen in reissendem Lauf auf Geröllboden in das Gebiet der Teichanstalt ein. Der Bach geht aber sodann bald in einen ruhigeren Lauf über. Der Lauf geht dann durch eine kanalisierte, bachähnliche Wildrinne mit grösseren, teichartigen Ausbuchtungen. Die Wildrinne ist nur bei den Teichen Stenfälle I—X einigermassen frei von Vegetation. Ursprünglich fanden sich hier nur vereinzelte Bestände aus *Potamogeton polygonifolius.* In den letzten Jahren ist aber die hindurch bedingte Einwanderung von *Carex rostrata* stellenweise sehr auffallend geworden. Die Wildrinne ist in ihrem jetzigen Aussehen erst durch die Regulierungen entstanden, die teichartigen Ausbuchtungen bewahren aber noch viele Züge ihrer Ursprünglichkeit.

Als Bestandbildner treten in den seichteren Partien der teichartigen Ausbuchtungen die folgenden Arten auf: *Calla palustris, Carex rostrata, Equisetum fluviatile, Glyceria fluitans, Juncus supinus* f. *fluitans, Menyanthes trifoliata, Myriophyllum alterniflorum, Nuphar luteum.*

Die Stromgeschwindigkeit ist hier oft fast gleich null. Boden aus Torf- und Dymaterial.

Der Randabschnitt der teichartigen Ausbuchtung unmittelbar oberhalb der Laboratoriumschleuse geht sogar in ein kleines *Eriophorum*-Moor über.

Die teichartigen Ausbuchtungen, welche jetzt alle durch Schleusen reguliert sind, sind bei der Regulierung zu einem geringen Teil etwas vertieft. In diesen tieferen Abschnitten hört auch fast jede Vegetation schon bei einer Wassertiefe von etwa 0,5—0,75 m auf. Nur vereinzelte *Nuphar*-Bestände fristen noch ausserhalb dieser Tiefenzone ihr Leben.

Als Bestandbildner in der bachartigen Wildrinne treten vor allem *Juncus supinus* f. *fluitans* und *Potamogeton polygonifolius* auf. Eine Besiedelung durch *Carex rostrata* und *Glyceria fluitans* tritt auch hier in der oben dargestellten Weise auf. — *Alisma Plantago aquatica* tritt seit einigen Jahren in dem Abschnitt bei den Stenfälle-Teichen vereinzelt auf.

Einige für diesen Abschnitt charakteristischen Vegetationsbildern, die alle im Jahre 1919 aufgenommen waren, sind auf Tafel IV—V zusammengestellt.

Fig. 15—16. Teichartige Ausbuchtung des Laufes bei den Hålls- und Såg-Teichen. Bestände von folgenden Pflanzen sind charakteristisch.

Calla palustris (auch vereinzelte grössere Bestände; vergl. Fig. 5).

Carex rostrata (massenhaft).

Equisetum fluviatile (spärlich).

Glyceria fluitans (allgemein).

Nuphar luteum (ziemlich allgemein).

Fig. 17. Die tiefste Stelle der genannten teichartigen Ausbuchtung oberhalb der Laboratorium-Schleuse. Maximale Tiefe hier etwa 1,5 m. Centrale Vegetation bis etwa 1 m nur aus vereinzelten *Nuphar*-Beständen.

6. Der Lauf hinter der Teichanstalt.

Der Bach verlässt die Teichanstalt durch das Randgebiet des Trollakärrmoors. Der Lauf ist hier zum grossen Teil von Birken und Erlen überschattet. Unter derartigen Voraussetzungen fehlt auch jede höhere Vegetation. Ihr photisches Optimum liegt sichtlich überhaupt sehr hoch, ein Umstand, der auch durch das vollständige Verschwinden der Vegetation bei jeder der zahlreichen Gebüsch-Überdachungen — die vor allem hier, aber auch vereinzelt im Oberlauf des Baches vorkommen — konstatiert werden kann.

B. Der Förhult-Bach.

Der Förhult-Bach beginnt mit einem Fall über Felsen und Steine und fliesst dann in einer kanalisierten Moorgegend. Als Bestandbildner treffen wir hier vor allem: *Carex rostrata*, *Glyceria fluitans*, *Juncus supinus* f. *fluitans*, *Nuphar luteum* und *Potamogeton polygonifolius*. Die Verteilung der Bestände folgt der Stromgeschwindigkeit in der früher für den Fiolen-Bach dargestellten Weise.

Durch einen teilweis gebüschüberdachten, fast sterilen Lauf zwischen Stein und Geröllen ergiesst sich der Förhult-Bach dann in den Skärsmo-Bach.

C. Der Skärsmo-Bach.

Der Skärsmo-Bach verlässt den regulierten S. Skärsmo-See durch einen gesprengten, gebüschüberschatteten Kanal.

Nachdem der Bach sodann den alten, nunmehr verlassenen Mühlenteich bei Skärsmo passiert hat, tritt er in seiner ursprünglichen Natur auf. Es ist dies entweder ein Stein- und Geröllauf oder auch ein Serpentinlauf durch die Sümpfe. Als Bestandbildner finden wir hier: *Carex rostrata*, *Glyceria fluitans*, *Juncus supinus* f. *fluitans*, *Potamogeton polygonifolius*. Die Verteilung der Bestände wird wie gewöhnlich durch die Strömungsverhältnisse geregelt. Von den genannten Pflanzen spielt vor allem der *Juncus* hier eine grosse Rolle. Da diese Pflanze leicht weggerissen und dann mit dem Wasser weiter transportiert werden kann, so werden auch neue Laufabschnitte — wenn die Naturverhältnisse sonst zugänglich sind — bald hierdurch besiedelt. Der genannte Umstand macht sich übrigens auch in rein praktischer Hinsicht für den Wassermühlenbetrieb geltend. Wenn die *Juncus*-Drift im Gang ist, muss nämlich die Reinigung der Schleusen-Gitter besonders beachtet werden.

D. Der Eskås-Bach.

(Vergl. Tafel V.)

Nach dem Zusammenfluss der Skärsmo- und Förhult-Bäche zeigt der Bachlauf noch immer dieselbe Physiognomie, welche wir für den Unterlauf des Skärsmo-Baches charakteristisch fanden.

Ausser den oben besprochenen Bestandbildnern treten indessen hier noch die folgenden hinzu: *Equisetum limosum*, *Nuphar luteum*, *Phragmites communis* und *Scirpus lacustris*.

Mit dem Sägemühlenteich bei Eskås scheiden die eigentlichen reophilen Bestände (*Juncus supinus* f. *fluitans* und *Potamogeton polygonifolius*) aus. Es treten aber auch einige neue Bestandbildner hier auf. Wir haben demnach hier mit den folgenden Bestandbildnern zu rechnen: *Carex rostrata*, *Equisetum limosum*, *Isoëtes lacustre*, *Lobelia dortmanna*, *Naumburgia thyrsiflora*, *Nuphar luteum*, *Scirpus lacustris*.

Der Bachlauf läuft dann mehr oder weniger kanalisiert in das Randgebiet des Trollakärr-Moors ein. Die wesentlichsten Bestandbildner sind hier *Carex rostrata*, *Equisetum limosum*, *Glyceria fluitans*, *Juncus supinus* f. *fluitans*. Von diesen Beständen gehören wie gewöhnlich die erst- und die letztgenannte nur den ruhigeren Abschnitten an.

In dem Moorlauf finden wir, je nach den Strömungsverhältnissen, die folgenden Bestände ausgebildet: *Carex rostrata*, *Equisetum limosum*, *Glyceria fluitans*, *Juncus supinus* f. *fluitans*, *Potamogeton polygonifolius*, *Sparganium ramosum*, *S. simplex*.

Einige für diesen Abschnitt charakteristische Bilder sind auf Tafel V zusammengestellt.

Fig. 18. Geröll-Lauf des Eskås-Bachs unmittelbar oberhalb des Sägenmühlenteiches bei Eskås. Einzige (submerse) Zentralvegetation: *Juncus supinus* f. *fluitans* und *Potamogeton polygonifolius*.

Fig. 19. Derselbe Abschnitt. Hier eine spärliche Vegetation aus *Scirpus lacustris*.

Fig. 20. Ausflussgraben des Sägemühlenteiches bei Eskås. Grosse centrale Vegetation aus *Juncus supinus* f. *fluitans* mit sekundärer Besiedelung von *Carex rostrata*.

E. Der Aneboda-Bach.

Nach der Vereinigung der zwei Bachläufe von Fiolen und Eskås tritt der Aneboda-Bach zuerst in einem Moorlauf von oben gegebener Charakteristik auf. Er mündet nach einigen Stauteichen und Fällen (Mühlenteich bei Aneboda, Sägeteich bei Aneboda) über Stein und Felsen durch einen Geröll-Lauf in den Stråken-See. Der letztgenannte Lauf ist wegen der Regulierungen der Mühle- und Sägewerke fast vollständig steril.

F. Die allgemeinen Charakterzüge der Bachflora.

In der vorhergehenden Darstellung wurde nur die Flora des Fiolen-Baches etwas ausführlicher besprochen. Die Haupt-

faktoren, welche die Konstitution der oligotrophen Bachflora bedingen, scheinen mir nämlich schon damit klar zu liegen. Im Prinzip begegnet man auch in den übrigen Bächen demselben Bilde.

Versuchen wir indessen hier kurz die Hauptfaktoren in der Verbreitung der Bachflora zusammenzufassen, so ergeben sich die folgenden Schlussfolgerungen.

1. Als Hauptfaktor für die Verteilung der Bestände dürfte die Strömungsgeschwindigkeit zu betrachten sein.

In dieser Hinsicht können wir die Bestandbildner in der Weise, wie die beistehende Tabelle zeigt, gruppieren.

Tab. II. *Übersicht über die Verteilung der Bestände in ihrer Abhängigkeit von der Strömungsgeschwindigkeit.*

Art	Gefunden bei starker Strömung	Gefunden bei schwacher Strömung	Gefunden in ruhigem Wasser
Alisma Plantago aquatica		+	+
Calla palustris			+
Callitriche hamulata		+	+
» *stagnalis*		+	+
Carex rostrata		+	+
» *Hudsonii*			+
Glyceria fluitans		+	+
Equisetum limosum		+	+
Juncus supinus f. *fluitans*	+	+	+
Lobelia dortmanna	+	+	+
Menyanthes trifoliata		+	+
Myriophyllum alterniflorum		+	+
Naumburgia thyrsiflora		+	+
Nuphar luteum		+	+
Nymphæa alba		+	+
Potamogeton natans		+	+
» *polygonifolius*	+	+	
Phragmites communis		+	
Scirpus lacustris		+	
Spargania		+	+
Fontinalis dalecarlica	+	+	
Isoëtes lacustre		+	+

Die natürlichen Vorbedingungen werden indessen hier sehr oft durch die Besiedelung abgeändert. So finden wir vor allem, wie *Juncus supinus* f. *fluitans* und *Potamogeton polygonifolius* den Boden für weniger reophile Pflanzen bereiten. Bisweilen treten sie dann direkt als Pioniere auf. Diese haben dann

nicht nur den Boden für andere vorbereitet, sondern ihn auch für sich selbst unmöglich gemacht.

2. Von einer weit geringeren Bedeutung scheint die Bodenbeschaffenheit zu sein. Die beistehende tabellarische Übersicht gibt hierüber weitere Aufschlüsse.

3. Einen Spezialfall hierzu repräsentiert der Einfluss der Ockerablagerungen. Soweit ersichtlich spielt aber dieser Spezialfaktor keine verbreitungsbestimmende Rolle. Die beistehende Tabelle gibt hierüber weitere Aufschlüsse.

Tab. III. *Übersicht über die Verteilung der Bestände in ihrer Abhängigkeit von der Bodenbeschaffenheit.*

Art	Gefunden auf Dy- oder Torfboden	Gefunden auf Stein, Grus- oder Sandboden	Gefunden auf Ockerboden
Alisma Plantago aquatica	+	—	—
Calla palustris	+	—	+
Callitriche hamulata	+	+	+
» *stagnalis*	+	+	+
Carex rostrata	+	+	+
» *Hudsonii*	+	—	—
Equisetum fluviatile	+	+	+
Glyceria fluitans	+	+	+
Juncus supinus f. *fluitans*	+	+	+
Lobelia dortmanna	—	+	—
Menyanthes trifoliata	+	—	—
Myriophyllum alterniflorum	+	+	+
Naumburgia thyrsiflora	+	+	+
Nuphar luteum	+	—	—
Nymphœa alba	+	—	—
Potamogeton polygonifolius	+	+	+
Phragmites communis	+	+	+
Scirpus lacustris	—	+	—
Spargania	+	—	+

4. Eine Konkurrenz der Bestände macht sich nur durch den oben besprochenen Spezialfall der Kolonisation bemerkbar.

5. Die Lichtverhältnisse machen sich insoweit sehr auffällig bemerkbar, als die Gebüschüberschattung des Laufes die Vegetation des Wassers vollständig vertilgt. Im freien Wasserlauf dürften sie aber keine grössere Rolle spielen.

Vergleicht man die heutige Entwicklung der Vegetation der Bachläufe in ihrer Abhängigkeit von den Einwanderungs-

möglichkeiten aus den See- und Teichgebieten, so wird man erstens finden, dass einige Seepflanzen in das Bachsystem übergewandert sind.

Es sind dies die folgenden: *Nuphar luteum*, *Nymphæa alba*, *Phragmites communis*, *Scirpus lacustris*, *Lobelia dortmanna*, *Isoëtes lacustre*. In der Bachflora spielen nur die zwei erstgenannten Arten eine grössere Rolle. — Die angeführten 6 Pflanzen kommen alle in den Seen vor und verbreiten sich wahrscheinlich in erster Linie weiter durch die Bächen.

Die Bachassoziationen bestehen deshalb auch aus einer sehr geringen Anzahl wirklich reophiler Arten — *Juncus supinus* f. *fluitans*, *Potamogeton polygonifolius* — mit denen sich vor allem einige Teichformen mischen. Ein näheres Studium der in der Tabelle S. 6—7 mitgeteilten Daten dürfte dies näher beleuchten.

IV. Die Teichflora.

A. Die Teichtypen und ihre Entwicklung.

(Vergl. Tafel VI.)

Als Versuchsanstalt für Karpfen- und Schleienzucht verfügt die Teichanstalt bei Aneboda über drei verschiedene Teichtypen. Es sind dies die folgenden: Die Brut-, die Abwachs- (Sommer-) und die Winterteiche. Von diesen Teichen sind die erstgenannten — die übrigens sehr seicht (nur einige dm tief) sind — nur einige Wochen im Sommer, die letztgenannten — die übrigens die tiefsten (bis zu 3 m) Teiche der Wirtschaft darstellen — nur während der Wintermonate bespannt. Bei einer Besprechung der Wasservegetation scheiden sie deshalb aus. Als Gegenstand dieser Untersuchung kommen deshalb nur die Abwachsteiche in Frage.

Die Abwachsteiche der Karpfen- und Schleienzucht sind in limnologischer Hinsicht als periodische Teiche mit stagnierendem Wasser zu bezeichnen. Sie sind im allgemeinen von Anfang Mai bis Mitte oder Ende Oktober bespannt, liegen aber in den Wintermonaten trocken. Der Boden friert dann mehr oder weniger vollständig durch. In Ausnahmefällen werden diese Teiche auch einer sommerlichen Durchtrocknung ausgesetzt.

Es liegt auf der Hand, dass diese Kulturtechnik einen wesentlichen Einfluss auf die Tier- und Pflanzenwelt des Wassers und des Bodens ausübt. Nur eine sehr geringe Anzahl dieser theoretisch wie praktisch gleich wichtigen Fragen sind indessen bis jetzt näher studiert.

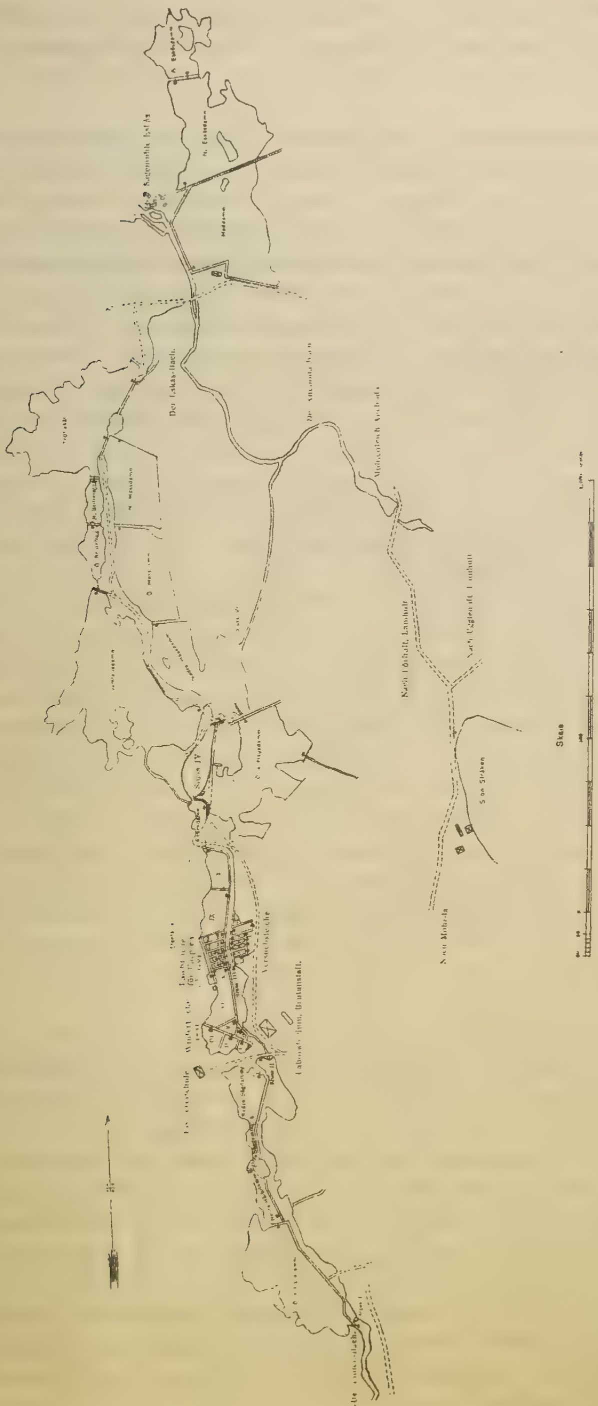

Fig. 2. Karte über die Teichwirtschaft bei Aneboda 1916.

Der Teichbau bei Aneboda begann im Jahre 1906. Zur Zeit verfügt die Anstalt über 6 Brut-, 6 Winter-, 19 Abwachs- und 7 Versuchsteichen. Vergl. übrigen die voranstehende Karte.

Die Abwachsteiche, mit denen wir hier ausschliesslich zu tun haben, sind durchgehends auf Moorboden gebaut. Im allgemeinen ist dieser Boden verhältnismässig fest. Ein Aufschwämmen des Bodens, wodurch grössere Schwimminseln gebildet werden, hat nur in Ausnahmefällen stattgefunden. Die Teiche sind z. T. durch natürliche, zum grössten Teil aber durch künstliche Dämme von einander getrennt. Diese Dämme, welche oberflächlich aus Grus bestehen, sind bei uns nicht pflanzlich angebaut. Eine reiche Vegetation aus Erlengebüsch hat sich aber während des Laufes der Zeit daran angesiedelt. Die Abwachsteiche sind ziemlich seicht. Die mittlere Tiefe beträgt höchst 1 m. Der Boden ist von einem Grabensystem durchgezogen, das im Abfischgraben vor dem Ablassmönch seine höchste Tiefe aufzuweisen hat. Diese höchste Tiefe geht niemals über einige m.

Die Teiche werden im Frühling allmählich mit Wasser vom Bachlauf aus gefüllt. Die Ablassung erfolgt ebenso im Herbst allmählich durch Ziehen der Bretter beim Abfischmönch.

Wie schon einleitend bemerkt, sind alle Teiche Anebodas auf Moorboden gebaut. Zum Teil waren hier früher versumpfte Wälder, flache *Carex rostrata*-Sümpfe oder sogar Randgebiete des grossen Hochmoores Trollakärr.

Die von der Teichwirtschaft veranlasste Aufstauung des Wassers bedingte deshalb auch ursprünglich eine sehr geringe Entfaltung der höheren Vegetation. Schon nach einigen Jahren war aber die Besiedelung im Gang. Hierbei beteiligten sich in erster Linie *Carex rostrata*, *Glyceria fluitans* und *Potamogeton natans*.

Einige Bilder, welche einen Teil der hier abgehandelten Verhältnisse etwas näher beleuchten, sind auf Tafel VI zusammengestellt. Es zeigen von den Bildern:

Fig. 21. Charakteristische, mit Rücksicht auf die höhere Vegetation sterile Wasserfläche eines neu angelegten Teiches. (Övre Mossdammen, 1921.) Der Teich ist in dem Randgebiet des grossen Hochmoors Trollakärr gelegen. Spärliche Randkolonisation durch *Carex rostrata*.

Fig. 22. Teich mit auftreibendem Torfboden (Nedre Hagadammen, Juni 1917). Diese Schwimminseln entbehren im allgemeinen jeder Vegetation. Eine Kolonisation durch *Carex rostrata* kann jedoch eintreten.

B. Die jetzige Zusammensetzung und die Entwicklung der höheren Pflanzenvegetation der Teiche.

(Vergl. Tafel VI—VIII.)

Die Zahl der Arten, welche sich bei der Zusammensetzung der jetzigen Wasservegetation Anebodas beteiligen, ist eine sehr geringe.

Ein Teil von diesen Arten bildet sehr grosse Bestände, ein anderer Teil aber nur sehr kleine. Gewisse Bestände sind überall verbreitet, andere treten nur an sehr begrenzten Lokalitäten auf.

Über die jetzige Stellung der Teichvegetation gibt die beistehende nach diesen Gesichtspunkten geordnete Tabelle nähere Aufschlüsse.

Nach den Erfahrungen, die ich bei neu angelegten Teichen gemacht habe, scheint es im allgemeinen jedenfalls einige Jahre dauern, bis sich eine eigentlich bestandbildende Wasserflora entwickelt hat. Hierbei haben immer die Arten *Carex rostrata*, *Glyceria fluitans* und *Potamogeton natans* die Hauptrolle gespielt. Eine vollständige Verwachsung kann durch diese Arten, u. zw. jede für sich — aber auch kombiniert — stattfinden.

Von diesen Arten sind die erst- und letztgenannte als die konkurrenzkräftigsten zu bezeichnen. Die Erfahrung hat auch gelehrt, dass eine mehr oder weniger vollständige Verwachsung der Teiche schon nach etwa 10 Jahren hierdurch stattfinden kann.

Trotz der winterlichen Trockenlage entwickeln die Teiche Jahr für Jahr fast dieselbe Flora wie früher, aber stets in verstärkter Ausbildung. Es erklärt sich dies leicht aus dem Umstand, dass alle Arten der Hauptassoziationen mit kräftigen, in Schlamm lebenden Wurzelsystemen ausgerüstet sind. Sie können auch, entweder in diesem Zustand oder auch als periodische Landpflanzen (die Schwimmblattformation überhaupt!), eine sommerliche Trockenlage der Teiche gut durchleben.

Trotz dieser Verhältnisse sind es aber bis jetzt nur einige Teiche, die vollständig verkrautet waren. Es sind dies einige von den ältesten und z. T. kleinsten der Teiche der Anstalt.

Das allgemeine Aussehen der Teiche im Sommer 1922 ist in grossen Zügen — mit Rücksicht auf die Hauptbestände — tabellarisch zusammengestellt S. 22—23. Wie daraus ersichtlich, sind es nur ganz wenige Pflanzen, welche auch quantitativ eine grössere Rolle spielen. Die sowohl in qualitativer wie in quantitativer Hinsicht geringe Bedeutung der eigentlichen Seenformen (vergl. Tab. S. 6—7 und S. 22—23) ist höchstauffallend.

Tab. IV. *Die Verbreitung der Arten im Teichgebiet bei Aneboda 1922.*

Bestände	Allgemeine Verbreitung	Lokale Verbreitung	Bemerkungen
1. Bestände von grösserer Flächenausdehnung			
Alisma Plantago aquatica		+	Trat zuerst vor mehreren Jahren in dem Teich Jämfälledammen auf. Beginnt sich dort immermehr zu verbreiten. — Im Jahre 1921 dazu in den Teichen Stenfälledammen Nr. X und Brittelagg sehr häufig.
Carex rostrata	+		
Glyceria fluitans	+		Vereinzelt in dem Bach bei den Stenfälleteichen.
Potamogeton alpinus		+	Nur in den Teichen Nedre Sågdammen, Stenfälledammen X, Trollakärrdammen. Dort aber seit mehreren Jahren.
» *natans*	+		
Typha latifolia		+	Nur in den Teichen Jämfälledammen und Maddammen. Dort aber seit mehreren Jahren.
Amblystegium Kneiffii		+	Seit mehreren Jahren vor allem in dem Teich Jämfälledammen massenhaft entwickelt.
» *exannulatum*		+	Seit einigen Jahren in dem Teich Övre Brittelaggdammen.
2. Bestände von geringerer Flächenausdehnung.			
Calla palustris	+		
Callitriche hamulata und *stagnalis*		+	Ziemlich allgemein.
Lemna minor		+	Sehr selten. Entwicklung sehr gering.
Lobelia dortmanna		+	Nicht im Hauptgebiet, wohl aber im Nebengebiet (Nedre Eskås) vorhanden.
Naumburgia thyrsiflora		+	Ziemlich allgemein.
Nuphar luteum	+		
Nymphæa alba		+	Nicht im Hauptgebiet, wohl aber im Nebengebiet vorhanden.
Potamogeton pusillus		+	Sehr selten.
Scirpus lacustris		+	Nur auf einem Lokal gefunden.
Sparganium simplex	+		
Utricularia minor	+		

Tab. V. *Die Vegetation der Teiche bei Aneboda 1922.*

Teich	Gebaut im Jahre	Areal	Standpunkt im Sommer 1922
Övre Hållsdammen	1908	2,89	Die *Carex rostrata*-Bestände beherrschten ca. 1/3 der Fläche. Hauptentfaltung im S. W. Ausserhalb dieser Vegetation ein breiter Gürtel aus *Potamogeton natans*.
Nedre »	1908	0,46	Abgelassen wegen drohender Verkrautung durch *Carex rostrata* und *Potamogeton natans*. Vor allem in dem Teich Övre Sågdammen war die Verkrautung in den letzten Jahren fast über die ganze Wasseroberfläche gegangen.
Övre Sågdammen	1909	0,31	
Nedre »	1908	0,85	
Stenfälle IX. . .	1908	0,49	Bestände aus *Carex rostrata* und *Potamogeton natans* decken ca. 1/2 der Fläche.
Stenfälle X. . .	1908	0,36	Bestände aus *Alisma Plantago aquatica*, *Carex rostrata* und *Potamogeton natans* decken fast die ganze Fläche.
Jämfälle	1906	6,00	Bestände aus *Alisma* und — vor allem — *Carex rostrata* decken inselartig etwa 1/3 der Fläche. — Grosse submerse Bestände aus *Amblystegium Kneiffii*.
Övre Brittelagg .	1907	0,66	Bestände aus *Alisma*, *Carex rostrata* (hauptsächlich) und *Potamogeton natans* decken etwa 1/4 der Fläche. — Im Jahre 1923 ziemlich grosse submerse Bestände aus *Amblystegium exannulatum*.
Nedre » .	Schon vorhanden 1906	0,37	Die *Carex rostrata*-Bestände beherrschen fast die ganze Fläche.
Trolla-Kärr . . .	1907	5,00	Die *Carex rostrata*-Bestände decken etwa 1/3 der Fläche.
Övre Hagadammen	1910	2,47	Nur kleinere Bestände aus *Carex rostrata*, *Glyceria fluitans* und *Potamogeton natans*.
Nedre »	1914	4	Ebenso.
Övre Mossdammen	1915	1,5	Nur kleinere Bestände aus *Carex rostrata* und *Glyceria fluitans*.
Nedre »	1915	1	Ebenso.
Maddammen . .	1911	4,50	Wasserstand fast immer wegen Wassermangel gering. Grosse Randvegetation aus *Carex rostrata* und *Glyceria fluitans*. In der freien Wasserfläche in dem Övre Eskås-Teich ein kleiner Bestand aus *Potamogeton natans*. *Juncus sup.* f. *fluitans* allgemein. In dem Madteich kleinere Assoziationen aus *Nuphar*, *Nymphæa*, *Typha*.
Övre Eskåsdammen	1906	0,78	
Nedre »	1906	2,90	

Eine Reihe von Bildern, welche diese Verhältnisse näher beleuchten, ist auf den Tafeln VI—VIII zusammengestellt. Im Einzelnen zeigen die Bilder folgendes:

Fig. 23—24. Die Bilder zeigen einige Beispiele von der Verkrautung eines Teiches (Stenfälle X, 1922) durch mehrere fleckenweise für sich auftretende Bestände.

Fig. 23. Wie aus dem Photo — von S aufgenommen — ersichtlich, spielt bei dem Verkrauten des Teiches *Carex rostrata* die Hauptrolle. Diese Bestände ist fast von Anfang an in dem Teich gegenwärtig gewesen.

Fig. 24. Neben der *Carex rostrata*- spielen die *Potamogeton natans*-Bestände, welche erst in den letzteren Jahren eine grössere Bedeutung erreicht haben, jetzt die Hauptrolle. — Die *Alisma*-Bestände, welche überhaupt erst in den letzten Jahren hier eingewandert sind, sind noch ziemlich begrenzt in ihrem Auftreten. Sie kommt noch hauptsächlich nur in der Nähe des Abflussmönches vor. Die Photographie ist von dem Damm beim Abflussmönch genommen.

Fig. 25—28. Die Bilder bieten einige Beispiele der Bestände von grösserer Flächenausdehnung, welche z. T. schon zu einer vollständigen Verkrautung der betrefffenden Teiche geführt haben.

Fig. 25. Fleckenweise Hochproduktion von *Amblystegium Kneiffii* im Teich Jämfälledammen 1917.

Fig. 26. *Carex rostrata*-Bestände des Teiches Nedre Britelaggdammen 1918.

Fig. 27. *Glyceria fluitans*-Assoziation des Teiches Stenfälle VIII 1917. Dieser Typus der Verkrautung dürfte, praktisch gesehen, zu den minder gefährlichen gehören.

Fig. 28. *Potamogeton natans*-Bestände des Teiches Övre Sågdammen 1917. Diese Bestände führten — trotz Abmähen der Vegetation — schon einige Jahre später zu einer vollständigen Verkrautung des Teiches.

Fig. 29—30. Erstes Auftreten und jetzige Entwicklung von *Alisma* in dem Jämfälle-Teich.

Fig. 29. Die Entwicklung im Sommer 1917.

Fig. 30. Die Entwicklung im Herbst 1921. — Die Ablassung ist im Gang. Die grossen Inseln sind fast vollständig durch *Alisma* aufgebaut.

Fig. 31—32. Der Hauptbestand von *Typha* in dem Jämfälle-Teich 1923 vor dem Aufstauen des Teiches.

Fig. 31. Allgemeines Übersichtsbild.

Fig. 32. Detailbild, die bodenbildende Bedeutung der *Typha*-Förna zeigend.

C. Die horizontale und vertikale Verteilung der Teichvegetation.

(Vergl. Tafel IX.)

Die Assoziationen der Teichvegetation treten, wie schon gezeigt wurde, im allgemeinen als ziemlich reine Bestände in grösseren oder kleineren Flecken neben einander auf. Eine eigentliche Zonation ist hier im allgemeinen nicht zu konstatieren. Natürlich tritt z. B. *Potamogeton natans* auf tieferen, *Carex rostrata* auf seichteren Stellen auf usw. Die Unebenheit des Teichbodens bedingt aber, dass im allgemeinen keine auffallendere Zonation in dieser Weise zustande kommt. Deshalb auch die für unsere Teichflora so charakteristische »unregelmässige» fleckenweise Verteilung der Bestände.

Die besprochene Verteilungsweise der Bestände dürfte ohne weiteres aus der Morphologie der Arten erklärlich sein. Dazu spielt die Konkurrenz auch hierbei eine gewisse Rolle.

In einer Hinsicht ist aber auch der Einfluss der Standortsbedingungen sehr auffallend. Es betrifft dies die Tiefengrenze der Vegetation. Diese Frage soll deshalb auch hier etwas eingehender besprochen werden.

Diese Tiefengrenzen der Vegetation sind in den Teichen dank der teichwirtschaftlichen Arbeitstechnik sehr leicht festzustellen. Verfolgt man nämlich im Herbst die Ablassung vom Abfischmönch aus, so können die fraglichen Grenzen ohne weiteres mit fortschreitender Senkung des Wasserspiegels auf dem Pegel abgelesen werden.

In dieser Weise wurden im Herbst 1921 die Tiefengrenzen einiger der wichtigsten Bestände festgestellt. Die bezüglichen Ergebnisse sind in der untenstehenden Tabelle zusammengestellt.

Tab. VI. *Die Tiefengrenzen einiger Arten in den Teichen Anebodas 1921.*

Art	Obere Grenze	Untere Grenze
Alisma Plantago aquatica	0,1 Meter	0,5 Meter
Callitriche stagnalis	0 »	0,2 »
Carex rostrata	0 »	0,3 »
Equisetum fluviatile	0,2 »	Mehr als 0,5 Meter
Glyceria fluitans	0 »	0,75 Meter
Myriophyllum alterniflorum	0,2	Mehr als 0,5 Meter
Nuphar luteum	0 »	1 Meter
Potamogeton alpinus	0,4 »	0,5 »
» *natans*	0,1 »	0,85 »
» *pusillus*	?	0,5 »
Sparganium simplex	0,2 »	0,5 »

Wie daraus ersichtlich hört überhaupt jede Vegetation bei einer Tiefe von etwa 1 Meter unter dem mittleren Wasserstand des Sommers auf. Eigentliche Submerse sind sehr selten und sind kaum unter $^1/_2$ m zu finden.

Diese Tiefengrenzen zeigen ganz besonders auffallend geringe Werte. In den humusmesotrophen Seen der Gegend fallen sie z. B. mindestens doppelt so gross aus. Es liegt wohl auf der Hand, dass diese Tiefengrenzen in einem Teichgebiet wie dem hier untersuchten kaum anders als durch photische Faktoren erklärt werden können. Eine ausführlichere Darstellung der Lichtverhältnisse der Gewässer Anebodas soll anderorts bald gegeben werden.

Eine Reihe von Bildern, welche die hier besprochenen Verhältnisse etwas näher beleuchten, sind auf den Tafeln IX—X zusammengestellt. Im Einzelnen ergibt sich hieraus folgendes:

Fig. 33—35. Diese Bilder zeigen Abwachsteiche bei der Abfischung.

Fig. 33—34. Der Teich Övre Hagadammen bei der Abfischung im Herbst 1921. Die Bodenfläche unterhalb 0,85 m ist vollständig steril.

Fig. 35. Die teichartige Ausbuchtung der Wildrinne bei dem Ö. Hagateich beim Ablassen 1921. Die Bodenfläche unterhalb 0,75 m ist vollständig steril.

D. Die Teichkultur in ihren indirekten Beziehungen zu der höheren Wasservegetation.

Die Teichkultur bedingt aus rein praktischen Gründen eine Reihe von Eingriffen in das Leben der Gewässer, die auch eine Reihe von biologisch sehr wichtigen Folgen als Nebeneffekt aufzuweisen haben. Es sind dies vor allem die folgenden Massnahmen: Die winterliche bezw. die sommerliche Trockenlegung, die Düngung und die Fütterung.

1. Die winterliche Trockenlegung.

Den gewöhnlichsten und grundlegenden Eingriff der Teichkultur in die Ökologie der Organismenwelt des Wassers stellt die winterliche Trockenlegung dar.

Dieses Kulturprinzip ist in erster Linie durch die rein praktischen Forderungen des teichwirtschaftlichen Betriebes begründet. Die Trockenlegung ist gewiss auch produktionsbiologisch in verschiedenen Hinsicht wohl motiviert.

Der Effekt der Trockenlegung auf die höhere Vegetation der Teiche war früher vollständig unbekannt. Wie wir aber hier gesehen haben, wird tatsächlich in dieser Weise eine immer zunehmende Vegetation in den Teichen jedenfalls durch die konkurrenzkräftigsten Arten — also hier *Carex rostrata*, *Glyceria fluitans* und *Potamogeton natans* — nicht verhindert.

2. **Die sommerliche Trockenlegung.**

Eine sommerliche Trockenlegung der Teiche, die vor allem produktionsbiologisch motiviert wird (Bodenmelioration!), wurde nur in Ausnahmefällen bei Aneboda durchgeführt.

Untersucht man aber dann im Herbst derartige den ganzen Sommer hindurch trockengelegte Teichflächen, so findet man, dass die meisten der Teichpflanzen gut durchgehalten haben. Vor allem gilt dies für *Potamogeton natans*, dessen kleine, charakteristische Landformen mit ihren lebhaft grünen Blättern an der Bodenfläche aufleuchten. Das Wurzelsystem senkt sich sehr tief — bis auf einer Tiefe von einigen dm für das horizontalgehende Wurzelsystem — in den Boden hinein.

Es ergibt sich somit hieraus die praktische Schlussfolgerung, dass ein zufälliges sommerliches Trockenlegen im Prinzip nicht die Vegetationsverhältnisse der Teiche abändert.

3. **Die Düngungs- und Fütterungstechnik.**

In welcher ganz grossartiger Ausdehnung derartige Einflüsse auf die Planktonentwicklung einwirken, habe ich zuerst (1924) eben in Aneboda näher nachgewiesen.

So weit ich finde, sind aber derartige Einflüsse bisher in Aneboda ohne Effekt auf die höhere Wasservegetation geblieben. Ich erkläre dies einerseits daraus, dass im grossen und ganzen die geprüfte Bodendüngung (im allgemeinen handelte es sich um Kalkung) gewiss allzu klein gewesen ist, um den Chemismus des Bodens verändern zu können. Im Gegensatz hierzu muss der Effekt der Fütterung auf den Chemismus des Wassers als ein sehr tief eingreifender bezeichnet werden. Dieser Effekt macht sich aber erst in der letzten Hälfte des Sommers bemerkbar und ist, wie schon hervorgehoben, der Hauptsache nach auf das Wasser begrenzt. Wenn der Effekt eintritt, hat aber die höhere Vegetation schon ihre höchste Entwicklung erreicht. Eine Nachwirkung für das folgende Jahr ist wegen der Abfischungstechnik im grossen und ganzen ausgeschlossen.

Es scheint mir aber sehr wahrscheinlich, dass ein Flora-Wechsel von oligotrophen zu eutrophen Typen auch auf dem Gebiet der höheren Wasservegetation in den Bereich der Mög-

lichkeiten fällt. Spezielle Untersuchungen in dieser Richtung sind sowohl aus theoretischen wie aus praktischen Gründen sehr erwünscht.

Fassen wir die hier besprochenen Ergebnisse des nebensächlichen Effektes der Teichkultur auf die höhere Wasservegetation kurz zusammen, so ergibt sich also, dass dieselben auf diesem Gebiet tatsächlich eine so geringe Rolle spielen, dass sie in praktischer Hinsicht vollständig vernachlässigt werden können. Es ist dies, wie schon angedeutet, ein höchst auffallender Gegensatz zu den Verhältnissen auf dem Gebiet des Planktons, wo diese Nebeneffekte eine eben in praktischer Hinsicht oftmals ganz vorherrschende Bedeutung erreichen.

E. Der Kampf der Teichwirtschaft gegen die höhere Vegetation.

Für die Teichwirtschaft spielt die höhere Vegetation der Teiche die Rolle eines höchst variablen produktionsbiologischen Faktors, welcher die Gesamtproduktivität erhöhen oder verringen kann. In dieser Hinsicht gelten ganz sterile Teiche als schlecht. Dasselbe gilt für die ganz verkrauteten. Zwischen diesen Extremen liegt das Optimum, das die Praxis zu verwirklichen strebt.

Ein derartiges Optimum dürfte sich unter rein natürlichen Voraussetzungen kaum stabilisieren können. Vielmehr strebt die primäre Besiedelung des Teichbodens durch die höhere Vegetation einem extremeren Klimax — über die vollständige Verkrautung der Teiche führend — zu.

Wie wir im Vorigen gefunden haben, ist dieses Stadium für N- und P-oligotrophe bezw. humusmeso- bis polytrophe Teiche auf Moorboden schon nach etwa 10—15 Jahre erreicht.

Es erhebt sich dann die Frage, welche Massnahme die Praxis einer derartigen Entwicklung gegenüber ergreifen kann. Im grossen und ganzen sind es zwei Wege, die hierbei betreten werden können: Die Abmähung der Sommerteiche und die Einführung der Wechselkultur.

1. Die Abmähtechnik.

Als teichwirtschaftlich schädlich können bei Aneboda in erster Linie die grossen Bestände von *Carex rostrata* und *Potamogeton natans* bezeichnet werden. Es ist auch deshalb mehrmals versucht worden, die weitere Entwicklung dieser Bestände durch Abmähen der Sommerteiche zu begrenzen. Eine weitere Verwertung des abgemähten Pflanzenmaterials als für Kompostierung und Teichgründüngung kann bei unseren Verhältnissen nicht in Frage kommen.

Die bei Aneboda in dieser Richtung gemachten Erfahrungen zeigen indessen, dass ein Abmähen — jedenfalls wenn sich um die Bestände aus *Potamogeton natans* handelt — höchstens für eine ganz kurze Zeit hilft. Die verwachsenden Teiche mögen so sorgfältig wie auch möglich — am besten im Sommer — abgemäht werden — im nächsten Jahr ist die überhandnehmende Vegetation wiederum da, vielleicht etwas schwächer, im allgemeinen aber sichtlich unverändert oder sogar vergrössert. Die weitere Entwicklung der *Carex rostrata*-Bestände dürfte aber wirklich durch eine sehr zielbewusst durchgeführte Abmähtechnik etwas verhindert werden können.

Es ist doch, wenn man mit so konkurrenzkräftigen Pflanzen wie *Carex rostrata* und — vor allem — *Potamogeton natans* zu tun hat, sicher dass schon nach etwa zehn oder fünfzehn Jahren die Teiche unter unseren Verhältnissen dadurch fast vollständig verwachsen werden. Die Abmähtechnik kann vielleicht die Entwicklung z. T. verzögern; sie kann sie aber nicht verhindern.

2. Die Technik der Wechselkultur.

Es erhebt sich dann die Frage, welcher Praxis die Teichtechnik dann zu folgen hat.

Es ist wahrscheinlich, dass in dieser Beziehung nichts auszurichten ist, wenn nicht die ganze Teichtechnik auf eine Wechselkultur zwischen Landwirtschaft und Wasserkultur umgelegt wird. Ein derartiger Betrieb gewährt auch aus anderen Gründen beträchtliche Vorteile. Er kann sogar in erster Linie produktionsbiologisch begründet werden. Da die Einführung dieser Technik indessen bei Aneboda vor allem als Mittel zur Vertilgung der früher allen anderen Massnahmen trotzenden Vegetationswucherungen motiviert wurde, mag deshalb eine kurze Besprechung derselben in diesem Zusammenhange stattfinden.

Bisher ist ein derartiger Betriebsplan noch nicht in Schweden befolgt worden. Die Teichanstalt bei Aneboda steht indessen jetzt vor der Verwirklichung eines derartigen Betriebsplans. Dessen Einführung ist während der letzten Jahre aus praktischen Gründen sogar beschleunigt worden.

Es liegt wohl auf der Hand, dass die Wasservegetation in dieser Weise wirklich innerhalb gewünschter Grenzen gehalten werden kann. Es ist aber eben so selbstverständlich, dass mit der Einführung derselben viele charakteristische Züge des jetzigen Vegetationsbildes verschwinden müssen. Einige Beispiele aus der Praxis der letzten Jahre bei Aneboda werden dies näher zeigen.

Die Teiche, die in dieser Hinsicht zuerst — und zwar

nach dem Vorschlag von meinem Kollegen, Dr. H. NORDQVIST — in Arbeit genommen wurden, sind die Hålls- und Såg-Teiche. Von diesen war besonders der obere Såg-Teich durch die Wucherungen von *Potamogeton natans* in teichwirtschaftlicher Hinsicht sehr verschlechtert.

Nach endgültigem Ablassen der alten Teiche wurde deshalb zuerst das alte Grabensystem im Teichboden ausgegraben, verbessert und vervollständigt. Es folgte dann eine Räumung des Bodens von alten Holzstrünken, Steinen usw. Hiermit könnte dann die rein landwirtschaftliche Praxis einsetzen. Zum ersten Mal trug dann im Jahre 1922 der alte Teichboden eine gute und reichliche HafErernte. Nachdem der Boden dann noch einige Jahre der Landwirtschaft gedient hat, wird die Teichwirtschaft wiederum einsetzen usw.

Einige in dieser Hinsicht beleuchtende Bilder sind auf den Tafeln IX—X zusammengestellt. Im Einzelnen zeigen die Bilder folgendes.

Fig. 36. Der Teich Övre Hållsdammen 1923. Nicht für das Jahr aufgestaut. Fast die ganze Teichfläche von *Carex rostrata* überwuchert.

Fig. 37. Der Teich Nedre Hållsdammen 1922. Die Aufräumung des Bodens zwecks landwirtschaftlichen Betriebes ist im Gang.

Fig. 38. Der Teich Övre Sågdammen 1922. Die Aufräumung ist fast vollgezogen.

Fig. 39—40. Der Teich Nedre Sågdammen 1922. Der Boden ist aufgeräumt, die Strünke dienen als Zaun und auf dem alten Teichboden blüht eine reichliche Hafererernte.

Es ist wahrscheinlich, dass diese zuletzt besprochene, bei uns früher nicht teichwirtschaftlich geprüfte Betriebstechnik einen erheblichen Fortschritt bedeutet. Ihre Anwendung wird auch eine Menge von neuen wasserbiologischen Problemen stellen. Sie wird aber gewiss auch eine tiefgehende Veränderung der ursprünglichen Vegetationsverhältnisse des Teichgebietes bei Aneboda mit sich bringen. Die vorliegende Abhandlung, welche die Entwicklung und den Standpunkt der Teiche bis 1923 kurz geschildert hat, wird sich dann hoffentlich auch als Vergleichsmaterial für künftige Untersuchungen verwertbar zeigen.

Lund, Botan. Laboratorium der Universität, Januar 1923.

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Tryckt den 18 mars 1924.

Uppsala 1924. Almqvist & Wiksells Boktryckeri-A.-B.

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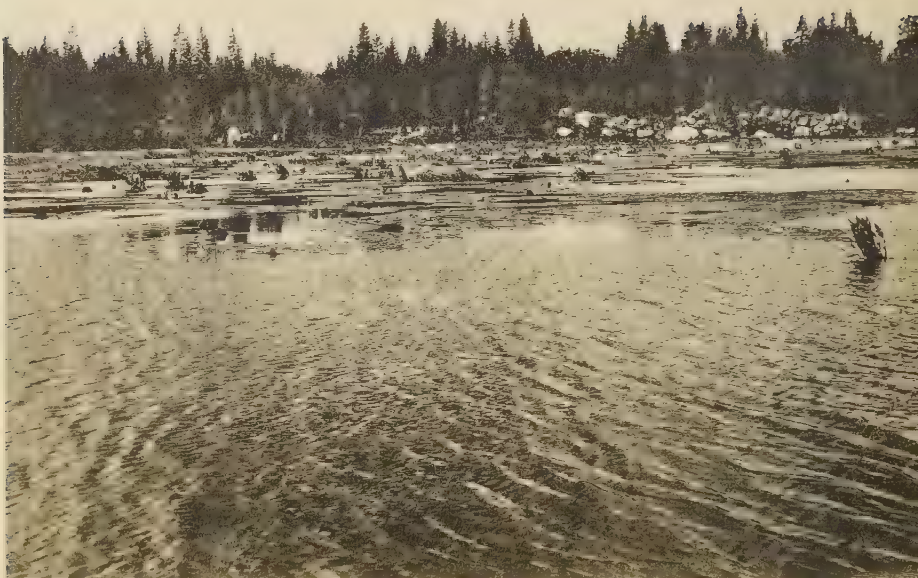

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ARKIV FÖR BOTANIK.
BAND 19. N:o 3.

On the Discontinuous Geographical Distribution of some Tropical and Subtropical Marine Algae.

By

NILS SVEDELIUS.

With 14 Figures in the Text.

Read November 28th 1923.

I. Introduction.

1. *The literature on the geographical distribution of the marine Algae in general very scanty and in many respects unreliable.*

Our knowledge of the geographical distribution of the marine Algae is at present to a great extent very incomplete. Notwithstanding the fact that numerous expeditions to far-off countries, as well as private botanists, have brought home large collections of marine Algae to our museums, it is remarkable to what a small extent the collected material has been dealt with from the point of view of plant-geography in general.

There is indeed no lack of works on the Algal vegetation from certain limited districts in Europe — particularly England, France and Scandinavia — and North America from a geographical point of view. But of the great oceans, regarded as units, one may say that only the Arctic Ocean has been the subject of methodical investigations from the point of view of its algal plant-geography, particularly by KJELLMAN (1883) and — as regards the coast of Greenland — by ROSENVINGE (1893, 1898). Plant-geographical papers, dealing with more or less limited parts of the extra-tropical Atlantic, have been written

for example by HARVEY (1852—1858), FARLOW (1881), COLLINS (1900), DAVIS (1913), and others on the coasts of North America; by HARVEY (1846—51), LE JOLIS (1863), HOLMES and BATTERS (1889, 1892), DEBRAY (1899), SIMMONS (1897, 1905), BÖRGESEN (1902—05), JÓNSON (1901—04, 1912), and CHALONS (1905) on the northern part of the Atlantic including the Channel; by HOOKER (1845—47), HARIOT (1888), SKOTTSBERG (1907), GAIN (1912), and COTTON (1915) on the South Atlantic, only to mention some of the more important names. We have, as yet, no comprehensive paper on the geographical distribution of the marine Algae of some greater district of the extra-tropical parts of the Pacific Ocean. The publications of HOWE (1914), SETCHELL and GARDENER (1919—20), and their disciples on the marine Algae of the Pacific coast of South and North America as well as the works of some Japanese algologists, especially those of OKAMURA (1899—1903), YENDO (1902—19), and others, form, however, a preliminary basis for a work of this kind, which, it is to be hoped, will appear without much delay. Concerning the family of the *Laminariaceae* there already exists, as a matter of fact, a preliminary study to a plant-geographical account by SETCHELL (1893).

It is particularly evident that until quite lately the tropical marine floras have been very imperfectly studied from the point of view of geographical distribution. MARTENS (1866) seems to have been one of the first to try to make out comparative lists of species from the different tropical seas and to divide these, with respect to their marine Algae, into different sections. The next plant-geographical paper of importance concerning the Algae of the Tropics dates from the year 1893, when G. MURRAY published »A Comparison of the Marine Floras of the Warm Atlantic, Indian Ocean and the Cape of Good Hope». Some years before (1889) he had published his »Catalogue of the Marine Algae of the West Indian Region», and in the year 1893 appeared E. S. BARTON's »A provisional list of the Marine Algae of the Cape of Good Hope». In these works is shown for the first time the constantly recurring and very striking conformity between the real tropical Algae of the warm Atlantic (the West Indies) and the Indian and Pacific Oceans, isolated as they are from each other. An attempt at plant-geographical explanation of these facts was then also given by MURRAY (1891, 1893).

Some more lists of species concerning more limited tropical districts certainly exist; for example the valuable work of MAZÉ and SCHRAMM (1870—77) of the marine Algae of Guadeloupe, that of COLLINS (1901) of the Algae of Jamaica, and that of VICKERS (1905) of the Algae of Barbados, and — perhaps the most valuable — that of BÖRGESEN (1913—20) of the Algae of the

former Danish West Indies and the »Liste des Algues du Siboga» by Mme. WEBER VAN BOSSE (1913—23), only to mention some of the most important.

The American algologist SETCHELL (1917) was, then, right in saying, in his Presidential Address on »Geographical Distribution of the Marine Algae», to the Botanical Section of the American Association for the Advancement of Science in New York in the year 1916: »The progress of the knowledge of the marine Algae has been slow in comparison with that of most other groups of plants, and the progress of our knowledge of the geographical distribution has been slower still». The difficulties are quite evident. The special systematic determination of the marine Algae is still obscure on many points; and without a close and critical examination of the species, naturally no certain conclusions as to Algal plant-geography can be drawn.

When botanists first began to observe and describe the marine Algae, they took the characters of the species solely from their external morphology. Therefore, it was quite natural that the description could not be sufficiently clear and exact, and the consequence was, that one and the same species was often reported as having been found in all Oceans of the world. MARTENS (1866) could, in the work quoted above, give a long list of Algae, evidently misdetermined, which had in this way been wrongly declared to belong to the marine flora of the Indian Ocean. But as the anatomical structure of the marine Algae became more strictly investigated and as the diagnoses of genus and species was based upon this fact, it was evident that many of the »cosmopolitan species» existing in the most widely separated Oceans were in fact quite heterogenous and sometimes so dissimilar, that they have later had to be considered as separate genera. J. G. AGARDH (1862) was perfectly right in maintaining that »a great part of the statements about Algae occurring in widely distant seas is attributable to imperfect knowledge and wrong determinations caused thereby, and that the number of such species as are supposed to grow in widely distant seas will be diminished in proportion as the accuracy of the scientific determinations increases».

An instructive and illustrative example of this is, for instance, the red Alga *Scinaia furcellata* (TURN.) BIV. The genus *Scinaia* has lately been subjected to a profound critical study regarding species by SETCHELL (1914), from whose work »The Scinaia Assemblage» the following is quoted. The genus *Scinaia* was established in the year 1822 by BIVONA upon TURNER's *Ulva furcellata*. The first species, *Scinaia furcellata* (TURN.) BIVONA, was described by BIVONA on the basis of a specimen from the Mediterranean, while TURNER's *Ulva furcellata* was described

on the basis of a specimen from the North Sea, from Sheringham (Norfolk). In course of time, this *Scinaia furcellata* was reported from nearly all the seas of the world: from the Mediterranean; from the European and North American coasts of the Atlantic; from the tropical Atlantic (the West Indies); from the Indian Ocean (Cape of Good Hope, Ceylon—Australia); and from the Pacific (the Philippines, Japan—Australia, New Zealand—Chili, Peru—North America). *Scinaia furcellata*, therefore, would practically exist in nearly all tropical, subtropical, and temperate seas. However, after having treated the whole *Scinaia* assemblage monographically, SETCHELL has shown that all these reports of *Scinaia furcellata* from tropical and subtropical seas are due to wrong determinations, in so far as the type for the species, TURNER's original *Ulva furcellata*, is strictly confined to the Mediterranean, the Atlantic coasts of Europe, and the temperate Atlantic coast of North America (New England). All Algae from other seas, described as »*Scinaia furcellata*», are either other well defined species or even quite different genera.

On the other hand, the opposite view has been held, the basis of which is the fiction that the same species of Algae do not exist in far distant seas, so that as soon as an Alga is found far away from its original locality, a new species is created. I will only mention KÜTZING, whose name is well known to all algologists, as an example of this kind of taxonomy.

What I have now said will sufficiently prove that one has to cope with no small difficulties in determining the geographical distribution of the marine Algae and that all discussions on Algal geography must of course be based on a profound and critical treatment of the material.

The difficulties of maintaining this exactitude have been particularly great concerning the less known tropical Algae. Modern critical geographical monographs on the marine Algae of the tropics have been rare until quite lately. But now BÖRGESEN's elaborate work on the marine Algae of the former Danish West Indies, the fruit of many years' study, is complete. This abundantly illustrated monographic treatment of a tropical Alga-flora forms a good basis for comparison with the Alga-floras of other tropical seas. It is particularly tempting to make a comparison of the Algae of the West Indies with the marine Algae of the Dutch Indies which, owing to the great Dutch Siboga-Expedition in 1899—1900, have been more closely investigated than perhaps any other tropical parts of the Old World.

2. *The problem of discontinuity in algology. — The resemblance between the Alga-floras of the West Indies and the Indo-Pacific Ocean.*

On the basis especially of these modern works and of my own collections and observations from Ceylon from the year 1902—03, I am now going to deal with some problems of plant-geography which were first presented to me several years ago, as I began to study the Algae I had collected in Ceylon during the years 1902—03.

It has been long known that the tropical Algae of the Old and the New World — of the tropical Atlantic and Indian Oceans — show great conformity as to their genera and species. These purely tropical Algae are, however, isolated from each other, as the Algae of the southern points of the great African and South American Continents are by no means tropical. Neither at the Cape of Good Hope and at the south-western coast of Africa nor — and still less — at the far more southerly Tierra del Fuego are the conditions of the sea such as to favour the existence of any real tropical Algae. As to South Africa, which is only at the latitude of 39°, this is caused by cold antarctic streams, *e. g.* the Benguela-Stream, going along the west coast from the Cape northwards. The influence of these cold streams on the African coast is noticed far to the north of the Tropic of Capricorn. Thus for instance a *Laminaria*, *L. Schinzii* FOSLIE, is known to have been found within the purely tropical zone, at Walfish Bay just north of Capricorn. Another species, *L. pallida* GREV., occurs not rarely at Table Bay near the Cape together with — and as frequently as — other members of the family of the *Laminariaceae* as *Ecklonia buccinalis* (L.) HORNEM. (»In sinu Tabulari *Ecklonia buccinali* vix rarior et copiose in littora ab undis ejecta» according to J. E. ARESCHOUG (1852, P. 361). And the famous giant-kelp *Macrocystis pyrifera* (TURN.) C. AG. is, according to HOOKER, abundant at the Agulhas' Bank at the southern point of Africa. The occurrence at the south-west coast of Africa of these representatives of the family of *Laminariaceae* — a family characteristic of and reaching its culmination in the cold and temperate seas and which does not exist at all in the tropical seas — clearly shows that the marine Alga-flora in these parts is far from tropical.

As I have already mentioned, it was G. MURRAY (1893) in particular who took up the problem of the isolated existence in the tropical parts of the Atlantic (the West Indies) of a great number of species and genera of Algae which now chiefly occur in the Indian Ocean and the Pacific and which are quite lacking in the comparatively well-known flora of the Cape — and of course also in Tierra del Fuego.

3. MURRAY'S *explanation of the discontinuity: owing to changes of climate in former epochs. — Such changes can explain the present discontinuous distribution of some marine Algae. — The work on the Arctic Ocean by* KJELLMAN.

To explain this discontinuous distribution MURRAY (1891, 1893, P. 4) assumed that the Alga-flora of the Cape has formerly, during supposed warmer epochs, been of a more tropical character and that the two areas for tropical Algae might then have been united and formed one continuous belt. In other words: he explained the present discontinuity by a hypothetical climatic change, prior to which the marine Algae at the Cape were purely tropical.

It is evident — and it has been proved almost to a certainty regarding other parts of the world — that climatic changes during former epochs can account satisfactorily for the present spread of marine Algae. KJELLMAN (1883) in his great classical work »The Marine Algae of the Arctic Sea» has made a complete list of the Algae common to the North Atlantic and the North Pacific Ocean. Considerably more than half of these — according to KJELLMAN's statement of 1883, 58½ % — are also to be found in the Arctic Ocean. These arctic species have, then, a continuous distribution from the North Atlantic to the North Pacific through the Arctic Ocean. KJELLMAN supposed, on good grounds, that the Arctic Ocean has been a special centre of development for marine Algae, which were naturally forced southwards into the Atlantic and Pacific Oceans during the glacial epochs. When the ice melted away, the purely Arctic species were driven northwards again; a great number, however, were able to remain in the northern parts of the Atlantic and Pacific Oceans, thus forming a common Arctic feature in the Alga-floras of these parts, which now consist of a mixture of Arctic and more temperate elements.

On the other hand, species common to the North Atlantic and the North Pacific which do not exist in the Arctic Ocean are probably more southern types which migrated northwards during the warmer, post-glacial epochs (Cfr. SIMMONS, 1905; A. S. JENSEN and P. HARDER, 1910) and the localities of which then formed a continuous belt that was later on broken either by changes in the disposition of land and sea, by the waters of the Siberian rivers, or by climatic deterioration. An example of this kind of distribution is afforded by the brown Alga *Chorda filum* (L.) STACKH., common in our Scandinavian waters, which occurs in the North Atlantic, on the western coasts of Europe, on the north-eastern coast of North America, including that of Greenland, and on the coasts of Iceland and Spitzbergen; in the North Pacific on the coasts of Japan and Alaska, but

which does not at all exist in the Siberian and the American parts of the Arctic Ocean. To this group, as regards geographical distribution, belongs — together with several other Algae such as *Fucus vesiculosus* L., *Phyllaria dermatodea* (DE LA

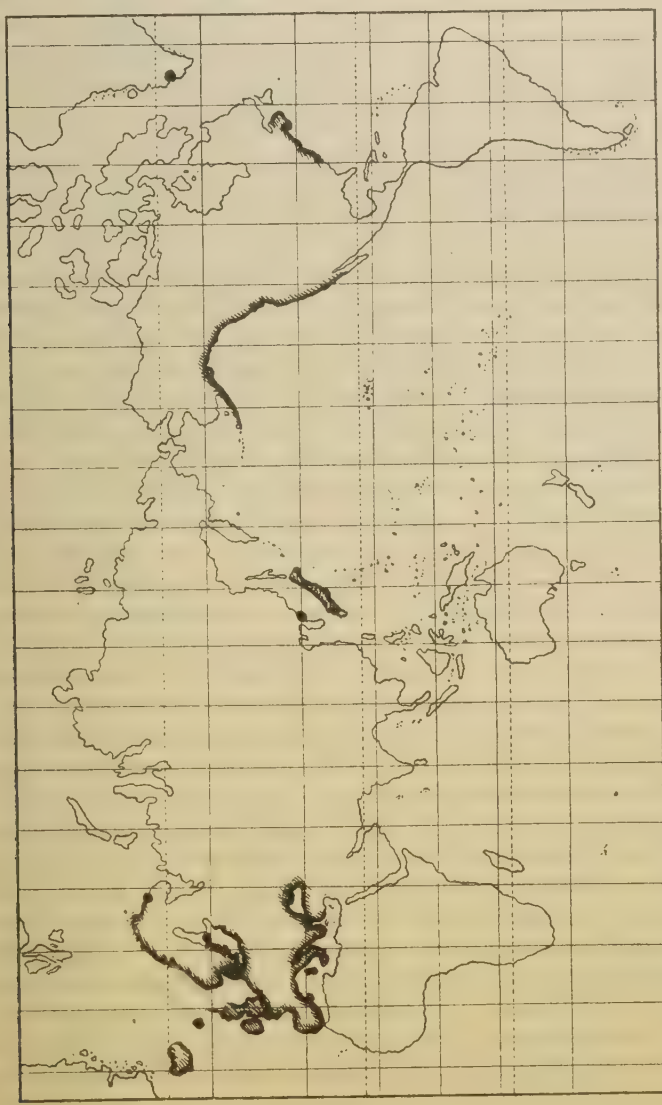

Fig. 1. The geographical distribution of *Zostera marina* (From OSTENFELD).

PYL.) LE JOL., and others (Cfr. SETCHELL, 1893 and SIMMONS, 1905) — the marine Phanerogam *Zostera marina* L. (Cfr. Fig. 1, reproduced from OSTENFELD, 1918).

Also the present discontinuous distribution of some marine

animals, for instance the Holothurian *Psolus squammatus*, the distribution of which has quite recently been dealt with by EKMAN (1923), seems to be most naturally explained in this way. It has been clearly shown that a thorough knowledge of the changes of climate etc. is necessary for a full comprehension of the present geographical distribution of the marine Algae of the northern Hemisphere, just as the knowledge of the geological development of a district is always a condition for the solution of its plant- and zoo-geographical problems.

4. *The geographical distribution of the marine Algae cannot fully be explained only by factors operating at the present time.*

The geographical distribution of plants in our time cannot, of course, be fully explained merely by the present climatic conditions and the present possibilities of distribution. Researches on these possibilities are, however, most instructive, as for instance has lately been shown concerning the Algae in SETCHELL's attempt (1917, 1920) to outline certain climatic zones for all the marine Algae, depending primarily upon the monthly mean temperature (isotheres and isocrymes) of the surface waters, with intervals of 5° C. This method explains many peculiarities concerning the distribution of Algae in the Oceans; but as a principle it does not suffice for the full explanation of the geographical distribution of the Algae. It is the same with the Algae as with land plants, that their real distribution is not always coincident with their possible distribution. As a rule, marine Algae do not possess the ability of many land plants to spread and be naturalised over great distances and open seas, and their possibilities of spreading with the currents or with ships have surely been rather over-estimated (Cfr. SIMMONS, 1897, 1905). This problem has lately (in 1918) been dealt with by SAUVAGEAU (1918) in an interesting paper »Sur la dissémination et la naturalisation de quelques Algues marines», in which he says: »Malgré l'uniformité du milieu dans lequel elles vivent, malgré leur transport par les courants, les bateaux, etc. . . ., les Algues marines se naturalisent assez rarement dans des localités, éloignées de leur habitat ordinaire». Nevertheless, removal and naturalisation actually do happen now and then and SAUVAGEAU gives us several instructive examples of this, which must not, however, be generalised.

5. *The impossibility of explaining the resemblance between the tropical Alga-floras in the West Indies and the Indo-Pacific Ocean only by factors operating at present times. — My explanation of 1905* (SVEDE-

LIUS *1906, a*) *founded upon the distribution of Caulerpa and the phanerogamic Sea-Grasses confirmed by* OSTENFELD (*1915*) *and* BÖRGESEN (*1920*).

If, then, it is evident that the present distribution of Algae as well as of other plants cannot be fully explained only by factors of the present time; and if we must therefore explain this distribution as the consequence of climatic and local changes in the relations between the algal associations caused thereby; then the question is: Have these climatic changes — these being, of course, as MURRAY (1893) suggests, unfavourable ones — caused the present geographical discontinuity of the purely tropical Alga-floras in the Atlantic and the Indian-Pacific Oceans?

In a lecture at Upsala in 1905 (SVEDELIUS, 1906 *a*, *b*) I maintained the improbability of this theory and brought forward another, more natural and nearer at hand: the fact that the present isthmus of Panama is comparatively new and that before it came into existence in the Miocene age, the whole Caribbean Sea was nothing but a great inlet of the Pacific Ocean. Then there was an open connection between the two tropical Alga-floras now separated by the isthmus of Panama.

The geology of Central America and particularly of the Panama zone has of late been subjected to a thorough geological investigation conducted by VAUGHAN (1919), and the most important datas of the history of this zone can easily be had from his publication, »Contributions to the Geology and Paleontology of the canal zone, Panama, and geologically related areas in Central America and the West Indies».

It is evident from this work (see Summary, P. 611), that the two oceans have at various periods been freely connected. The latest connection took place during the later tertiary (Pliocene) era; VAUGHAN says of it (l. c. P. 611): »Probably a narrow interoceanic connection, that admitted an Atlantic fauna into the present site of the Gulf of California». The first connection seems to have existed much earlier, already during the Triassic period.

An extensive interoceanic connection existed also during the later Eocene and during the Oligocene period.

VAUGHAN says about this:

Oligocene	upper . . .	Extensive submergence with interoceanic connections.
	middle . .	Maximum areal submergence with extensive interoceanic connections.
Eocene	upper . . .	Extensive submergence with interoceanic connections.

Eocene	middle	Apparently interoceanic connection across Central America.
	lower	Emergence of the Greater Antilles and Central America, no known interoceanic connection.

This shows that during the earlier (»lower») Eocene period no connection existed, but that a connection was formed during the later (»middle» and »upper») Eocene period, reaching its maximum during the following Oligocene period. Later, during the Miocene period, the continental Central American connection was formed between North and South America, by which the interoceanic connection was interrupted, though not entirely, as, according to what has been mentioned above, »a narrow interoceanic connection» seems to have existed during the following Pliocene age.

VAUGHAN also shows that a still earlier connection existed, during the Triassic (Upper, Karnic) and Jurassic times; but as this connection was totally cut off during the whole Cretaceous time (Createceous »upper» and »lower»), it can hardly be of any great importance for the explanation of the present distribution of the marine Algae. However, we must not wholly overlook the fact that types of the *Chlorophyceae* such as the verticillate *Siphoneae* have been found fully developed in the Carboniferous, Triassic, and Jurassic times already, though the now existing species do not seem to have appeared until Cretaceous times.

I have based my hypothesis of the interoceanic connection across Central America as an explanation of the present distribution of the marine Algae and the marine Phanerogams partly on the present distribution of the tropical algal genus *Caulerpa* but also on the tropical sea-grasses, viz. the genera *Thalassia, Cymodocea, Diplanthera* (syn. *Halodule*), and *Halophila*. All these genera show fine examples of so-called vicarious species, *i. e.* couples of systematically allied species, one of which usually is greatly spread in the Indian-Pacific Ocean, while the other only has a more limited distribution in the West Indies.

The general distribution of these marine sea-grasses is commonly known through the well-known work of ASCHERSON (1871). OSTENFELD (1915, 1917, 1918), who later also undertook a thorough study of the distribution of the marine Phanerogams, has afterwards fully adopted my theory (published as early as 1906), and I reproduce here (Fig. 2) from his work (1917) a map showing the distribution of the two species *C. isoëtifolia* ASCHERS. —*C. manatorum* ASCHERS. In this connection I may mention that in this work (also printed earlier in Proc. R. Soc. Victoria 27, N. S., Part II, 1915) OSTENFELD seems to put things not quite correctly in saying that I had based my theory on the

distribution of the genus *Caulerpa* only, while OSTENFELD was the first to have applied it to the marine sea-grasses.[1]

In my preliminary note, printed in Swedish (Bot. Not. 1906), as well as in my later work (1906, P. 106), printed in Ceylon in a publication perhaps but little known, I have emphasized the geographical distribution of the above mentioned Phanerogams as a confirmation of the theory in question. BÖRGESEN (1920) seems also to have overlooked the fact that I have not based my theory on the Caulerpas only, to judge from the way in which he treats this question in his work (l. c. P. 494). He,

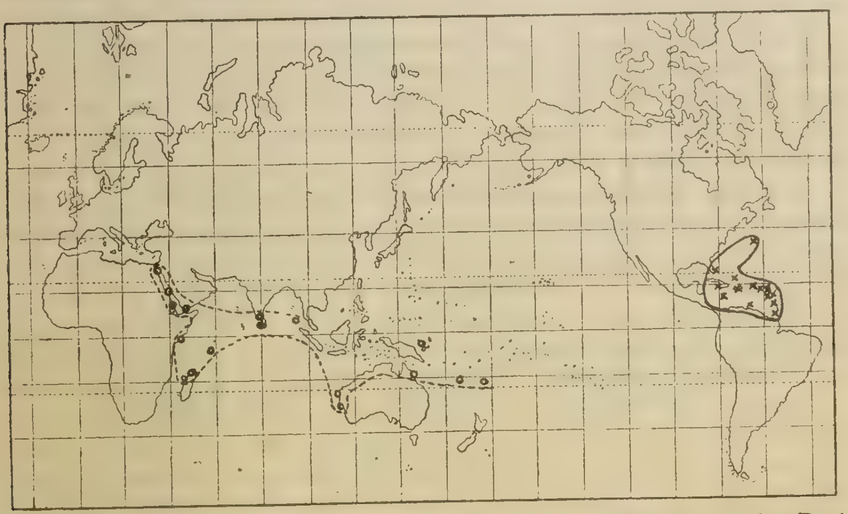

Fig. 2. The geographical distribution of *Cymodocea isoëtifolia* (Indian-Pacific) and *Cymodocea manatorum* (West Indian) (From OSTENFELD).

too, says that I have put forth this theory only to explain the distribution of the Caulerpas, while its application to the marine Phanerogams is called »OSTENFELD's conclusion» (l. c. P. 495), with quotations from OSTENFELD's works exclusively. As I have already pointed out, however, there is in OSTENFELD's publications of 1914 and 1917 nothing concerning the explanation

[1] OSTENFELD says for instance (1915, P. 189): »The peculiarities of distribution of the sea-grasses are not without parallel. Amongst the Marine Algae similar cases have been reported. GEORGE MURRAY (1873) has pointed out that there is a great resemblance between the algal flora of the Caribbean Sea and that of the Indopacific region. He supposes it to be explicable by a migration by way of the Cape. N. SVEDELIUS (1906) agrees with MURRAY as to the great resemblance of the floras, which he has himself studied, especially in *Caulerpa* (surely a very old type); but his explanation necessitates a water-connection where the Isthmus of Panama now is. This is essentially the same explanation as that I have offered with regard to the origin of the Caribbean sea-grasses». (Spaced out by the author!)

of the geographical distributions of the marine Phanerogams of the West Indies beyond what I had put forth as far back as the year 1906.

The above mentioned comprehensive work of BÖRGESEN on the Marine Algae of the West Indies (1920, P. 491) ends with a short account of the geographical distribution of this flora. A table (P. 492) shows that of the 327 species of the *Chlorophyceae*, *Phaeophyceae*, and the *Rhodophyceae* found in the former Danish West Indies about half the number or, to be exact, 161 have, so far, only been found in the West Indies or in neighbouring seas. Concerning the other 166 species, 112 are also known in the Mediterranean and on the European and African coasts of the Atlantic, while 111 occur in the Indian-Pacific Ocean as well. According to BÖRGESEN, then, the Alga-flora of the West Indies is composed of Atlantic as well as of Indian-Pacific elements.

A fact to be particularly considered is that, if the various classes of Algae are considered separately from this point of view, we find — as BÖRGESEN has clearly shown — that more than half of the 90 *Chlorophyceae* or, to be exact, 46 occur in the Indian-Pacific Ocean as well, while only 35 occur in the Mediterranean and other parts of the Atlantic. The corresponding numbers concerning the *Phaeophyceae*, 45 in all, are 18 and 14, and for the *Rhodophyceae*, 108 in all, 47 and 63. This means that the likeness to the Indian-Pacific flora is much greater regarding the *Chlorophyceae* taken by themselves than regarding the *Rhodophyceae* taken by themselves. This seems to me to be one of the most valuable and interesting results of BÖRGESEN's work, as it clearly confirms my theory of 1905 regarding the former interoceanic connection as an explanation of the geographical distribution of the marine floras — and why? Simply for the plain reason that among the *Chlorophyceae* themselves there are so many primeval types, particularly of the families *Siphonaceae* and *Siphonocladiaceae* — isolated, clearly limited genera with but a few species — while on the other hand the *Phaeophyceae* and especially the *Rhodophyceae* show a great many so-called critical genera with numerous species (as for instance in the family of *Rhodomelaceae*), evidently of a much younger date. If we accept the theory of a migration across Panama it is easily explained how those West Indian groups of Algae, where an active formation of species is going on in the present age, cannot be represented by the same species in the Indian-Pacific Ocean. They have evidently been formed after the interruption of the interoceanic connection, while the common types were formed before this break.

Thus also, BÖRGESEN has, like OSTENFELD, accepted my

theory, and they have not supported MURRAY's theory of an invasion via the Cape under hypothetical tropic periods of the sea at the southern point of Africa.

The whole question, however, seems to me to be of such great general interest from the plant-geographical point of view that I find it well worth a somewhat more detailed treatment than has been given to it in my earlier papers and in BÖRGESEN's work. This is so much the easier as we now have good material for comparison in the already published algological parts in the results of the Siboga-expedition.

In the following chapter I shall give a fuller exposition of this problem, particularly concerning the *Chlorophyceae*, because the treatment of this class already appears complete in the scientific works of the Siboga Expedition, and in another chapter I will touch on a similar problem viz. the resemblance that can be traced between the Mediterranean marine flora and that of the Indian and Pacific Oceans, which resemblance can also be traced in some few common marine organisms with now discontinuous distribution.

II. Comparison between the tropical Algae in the Atlantic and the Indian-Pacific Oceans.

1. Chlorophyceae.

The Algae of the order of *Chlorophyceae* which play a more prominent part in the marine vegetation belong almost exclusively to the groups *Ulothricales*, *Siphonocladiales*, and *Siphonales*.

A. Ulothricales.

The chlorophycean Algae now under consideration of the first of these groups are the practically cosmopolitan genera *Ulva* and *Enteromorpha* of the family *Ulvaceae*. *Ulva Lactuca* L. for instance has a most extensive distribution in nearly all the oceans of the world, at least in the Atlantic from the Arctic Ocean in the north down to the southern point of South America in the south. It has also been found — in any case the f. *latissima* (L.) LE JOL. — in the Indian and Pacific Oceans. The areas of distribution of this species in the two Oceans are connected by its unbroken occurrence at the southern points of the great Continents of South America and South Africa.

The same thing can most probably be said to hold good regarding the genus *Enteromorpha*.

Both these genera of the family *Ulvaceae* are critical ones with species of very delicate and vague characters. Their present

geographical distribution shows that no species — at least none of the former and very few of the latter — is to be found in the tropical Atlantic (the West Indies) which does not also occur in the Indian-Pacific Oceans, and their areas of distribution are continuous over the southern points of Africa and South America.

B. Siphonocladiales.

A much more interesting point is the distribution of the *Siphonocladiales*, a group more dominant in the warmer seas, with the exception, however, of the family *Cladophoraceae*, which just like the *Ulvaceae* is critical with many very similar and nearly related wide-spread species, the geographical distribution of which just owing to this circumstance is very uncertain.

With regard to geographical distribution the whole family of *Cladophoraceae*, like that of *Ulvaceae*, shows a great amplitude — they are evidently to a high degree eurythermal and euryhaline — so if species common to both Oceans occur it is very probable that their tropical areas of distribution communicate via the Cape or Tierra del Fuego.

1. Siphonocladiaceae.

On the other hand, the real tropical family *Siphonocladiaceae* affords much more interest from a plant-geographical point of view. This family may suitably be divided into two groups:

I) the first with the genera: *Cladophoropsis*, *Boodlea*, *Microdictyon*, and *Anadyomene*.
II) the second with the genera: *Siphonocladus*, *Struvea*, and *Chamaedoris*.

Boodlea.

The genus *Boodlea* for instance is represented in the Indian-Pacific district by about 4 species (WEBER VAN BOSSE, 1913) of which especially *Boodlea Siamensis* RBLD has an extensive distribution as far as from the Red Sea and the western coast of Africa in the west to the South Sea islands (at least to Samoa) in the east. This species is now also found in the West Indies (BÖRGESEN), but the genus is strictly tropical and is lacking at the Cape and of course also at Tierra del Fuego. Its present distribution is thus discontinuous and divided into two areas, one in the Atlantic, the other in the Indian-Pacific Ocean.

Microdictyon.

The genera *Microdictyon* and *Anadyomene* have a similar distribution to that of *Boodlea*. The best known species of *Microdictyon*, *M. umbilicatum* (VELL.) ZAN. has about the same

distribution as *Boodlea Siamensis* but is known from the eastern Atlantic as well (the western coast of Africa and from the south of Spain, Cadiz). Its Indian-Pacific district extends from the Red Sea to the South Sea islands including Hawai. On the eastern coast of Africa it is observed as far south as Durban (Natal Point, according to KRAUSS. Cfr. ARESCHOUG, 1851), but not at the Cape or western South-Africa. Probably another species is known from the Indo-Malayan Archipelago.

Anadyomene (Fig. 3).

Very interesting is the geographical distribution of the genus *Anadyomene* (Fig. 3). About half a dozen species are described of which at least 4 are so-called »good» species.

Among these *Anadyomene stellata* (WULF.) AG. occurs just as *Microdictyon umbilicatum* at several places in the West Indies (including Bermuda) and is also known from the Atlantic coast of South America as far south as Pernambuco, from the eastern Atlantic (Canary Islands), and from numerous places in the Mediterranean.

In the Indian-Pacific Ocean occur besides *A. stellata* some 3 species, of which *A. plicata* AG. seems to be rather common in the whole Indo-Malayan Archipelago. One species, *A. Brownii* (GRAY) J. AG., extends on the eastern coast of Australia about as far as the Tropic of Capricorn (Cfr. Fig. 3, P. 16). But regarding the genus *Anadyomene* it is a remarkable fact that in the Indian Ocean no species has as yet been found further west than Ceylon. This beautiful Alga would, to be sure, scarcely have escaped notice if it had really occurred at the eastern coast of Africa or in the Red Sea. Fig. 3 shows better than words the present discontinuous distribution of the genus.

It is to be noticed that the Atlantic has no species that is not also found in the Indian—Pacific Ocean.

Contrary to some other genera with discontinuous distribution, the *Anadyomene* just like the *Microdictyon* is rather common in the Mediterranean. The question now arises if these species have immigrated into the Mediterranean from the Atlantic, that is, from the west, or from any other direction? As the species is not known from the Red Sea, immigration in later times through the Suez canal need not be discussed. Moreover, the species in question was observed in the Mediterranean before the opening of that canal. In spite of this, the species may still have got into the Mediterranean from the east i. e. have immigrated into the Mediterranean during an early epoch when this sea had open connection with the Indian-Pacific Ocean during Tertiary times. That the Mediterranean to this very day really harbours marine plants which only in this way could have immigrated there is

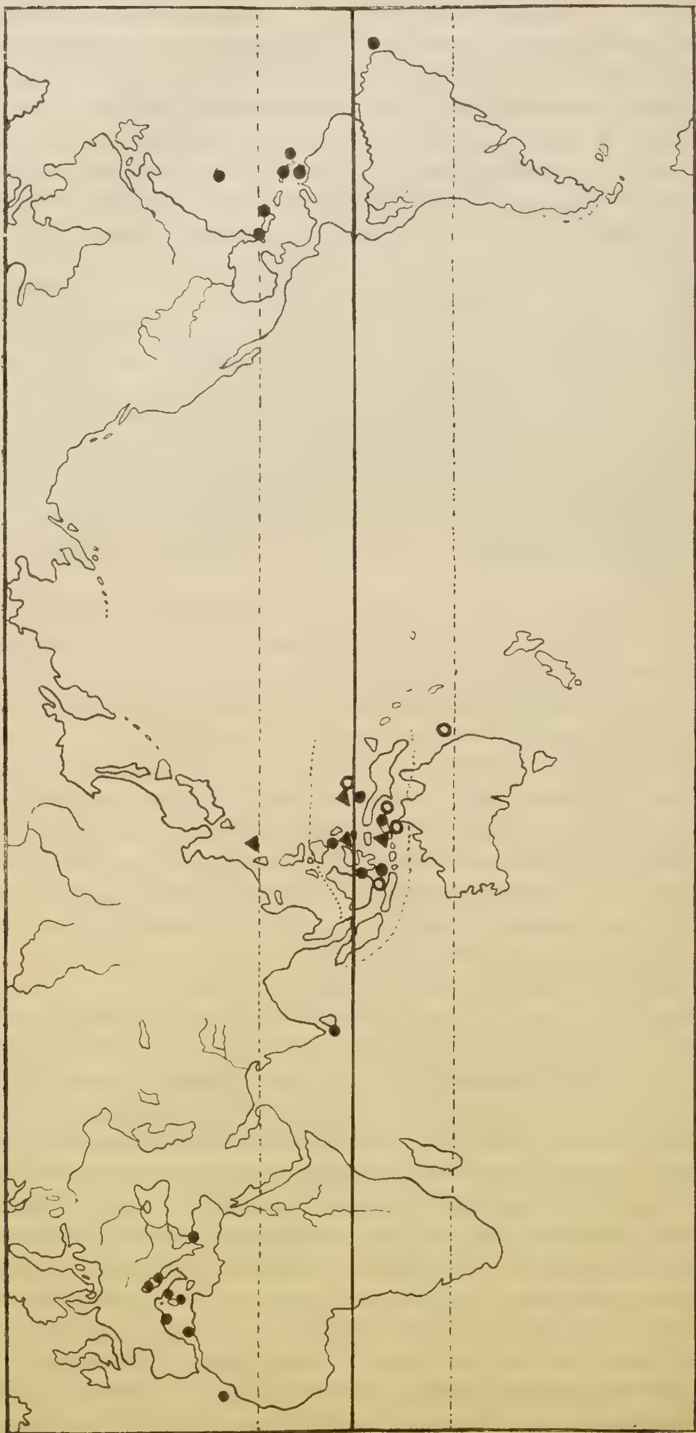

Fig. 3. The geographical distribution of *Anadyomene*.

● *A. stellata*, Indian-Pacific, Atlantic, Mediterranean. ○ *A. Brownii*, Indian-Pacific.
▲ *A. Wrightii*, Indian-Pacific. ..... *A. plicata*, Indian-Pacific.

indisputable — for instance the marine Phanerogam *Posidonia* — but this matter will be dealt with more in detail in a following chapter. Whether, then, *Anadyomene stellata* has come into the Mediterranean this way or from the Atlantic it is at present impossible to decide but must be left an open question. The discontinuity is in any case evident.

Struvea (Fig. 4).

The genus *Struvea* has a distribution nearly analogous to that of the *Anadyomene*, except that no species is to be found in the Mediterranean.

Str. anastomosans (HARV.) PICCONE is reported both from the West Indies and from the Indian-Pacific Ocean; in the latter ocean not farther west than Ceylon — thus not from the east coast of Africa.

In the West Indies there are also known 3 species in addition: *Str. elegans* BÖRGS., *Str. pulcherrima* (GRAY) MURRAY & BOODLE, and *Str. ramosa* DICKIE, the last mentioned perhaps not West Indian in the real sense as it is only known from the Bermudas and the Canaries, the only species of *Struvea* that is known north of the Tropic of Cancer.

From the Indian-Pacific district 2 other species are known from single localities, one of which, *Str. plumosa*, from South-West Australia, south of the Tropic of Capricorn.

A glance at the map (Fig. 4) shows the analogy regarding distribution between *Struvea* and *Anadyomene*. Neither genus is known from the coasts of tropical Africa nor from the Cape. Each genus is represented at the Canaries by one species, of which the *Anadyomene* species, but not the *Struvea*, also goes into the Mediterranean. Whether the real path for the immigration was from the west must for the present be left undecided (Cfr. above!).

2. **Valoniaceae.**

Valonia (Fig. 5).

The family of *Valoniaceae* is in the warmer Oceans represented by the genera *Valonia* and *Dictyosphaeria*, both belonging to the Green Algae which are most characteristic of the tropical seas. No coral reef either in the old or in the new world seems to be without at least one representative of these genera.

The morphologically simpler and more primitive genus *Valonia* (Fig. 5) contains little more than half a dozen good tropical species, 3 of which at least are common to the West Indies and the Indian-Pacific Ocean.

These common species are: *V. pachynema* (HARV.) V. MART.,

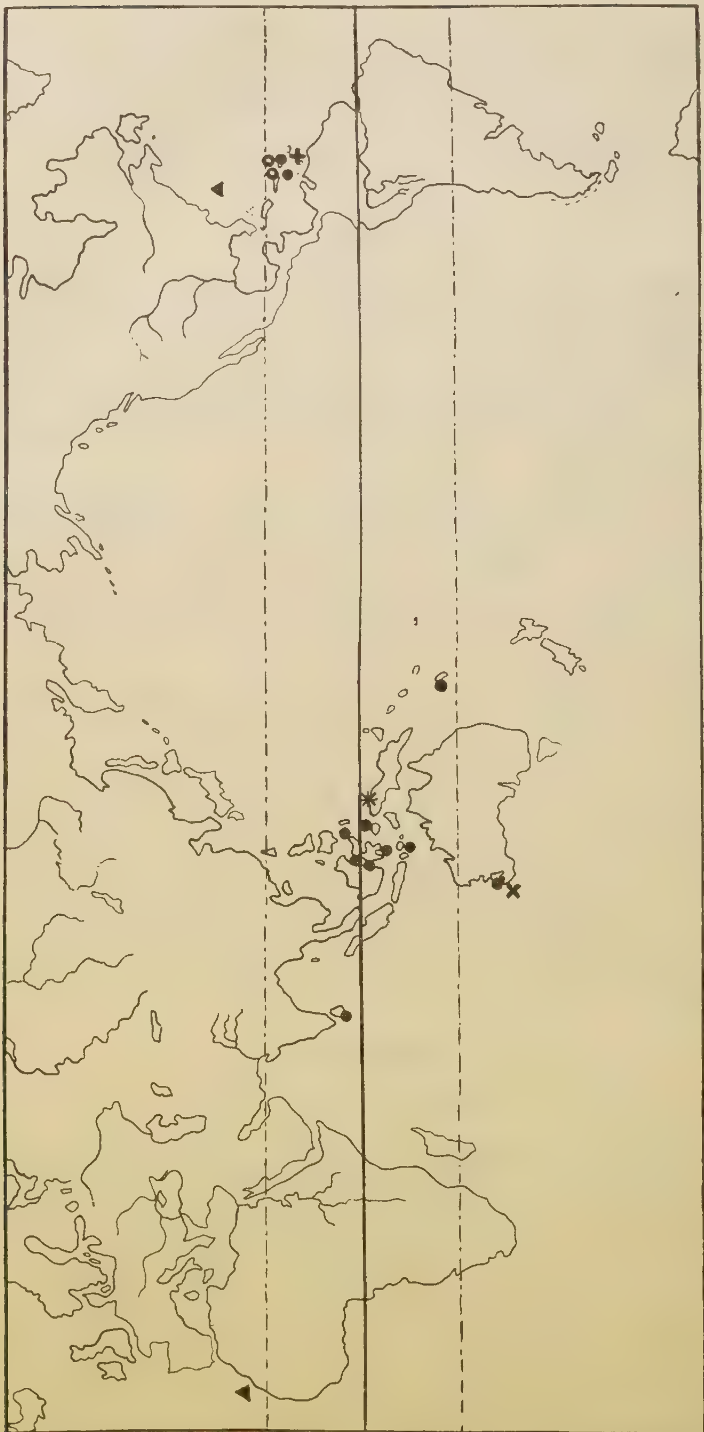

Fig. 4. The geographical distribution of *Struvea*.

● *Str. anastomosans*, Indian-Pacific, Atlantic. ○ *Str. elegans*, Atlantic.
× *Str. plumosa*, Indian-Pacific. ▲ *Str. ramosa*, Atlantic.
✳ *Str. tenuissima*, Indian-Pacific. + *Str. pulcherrima*, Atlantic.

V. utricularis (ROTH) AG., and *V. ventricosa* J. AG., of which *V. utricularis* is also known from the Mediterranean, from the Canaries, and from the south Atlantic coast of Spain (Cadiz). These common species — just as the great majority of Valonias — are quite lacking at the Cape and on the coasts of South Africa in general. Only off Madagascar in African waters do we meet again species of *Valonia*. The family seems — except the species which enter the Mediterranean and some single species in the temperate Atlantic — to be strictly limited to the tropical zone proper.

The Atlantic species seem — with the exception of *V. utricularis*, which is also North African and Mediterranean — to be limited to the West Indies (including Bermuda).

The West Indies harbours still another species, *V. macrophysa* KÜTZ., which is nearly related to *V. utricularis* and which is also found in several places in the Mediterranean as far in as the Adriatic.

In the Indian-Pacific Ocean *V. pachynema* is known from Ceylon in the west to Hawai and the Friendly Islands in the east. *V. utricularis* and *V. ventricosa* scarcely extend into the Indian Ocean but have their main distribution in the Malayan Archipelago — South Sea Islands. *V. ventricosa* is thus quite recently reported from Easter Island (BÖRGESEN, 1924).

In addition to the above mentioned common species, the Indian-Pacific area harbours 3 other species viz. *V. aegagropila* (ROTH) C. AG., *V. fastigiata* (HARV.) J. AG., and *V. Forbesii* J. AG. Of these *V. aegagropila* and *V. fastigiata* seem to have the most extensive distribution from Mauritius in the west to at least the Friendly Islands in the east. It is to be noticed that amongst these species only *V. aegagropila* is also known from the Mediterranean (Adriatic). *V. Forbesii* has about the same distribution but does not occur in the Mediterranean, and in the Indian Ocean it is not known farther west than Ceylon.

The most remarkable fact regarding the geographical distribution of the genus *Valonia* is the occurrence in the Mediterranean of no less than 3 species, of which one, *V. utricularis*, is common to the Atlantic and the Indian-Pacific Oceans, one, *V. macrophysa*, occurs in the tropical Atlantic only and one, *V. aegagropila*, in the Indian-Pacific Ocean only. On the other hand, no *Valonia* at all is known from South Africa and the Cape. The present discontinuous distribution of the genus is thus obvious (compare Fig. 5); but whether the Mediterranean species have immigrated from the east or from the west or from both these directions can now hardly be determined. Both possibilities are conceivable. The possibility must also be reckoned with that *V. macrophysa*, common to the Mediterranean and the

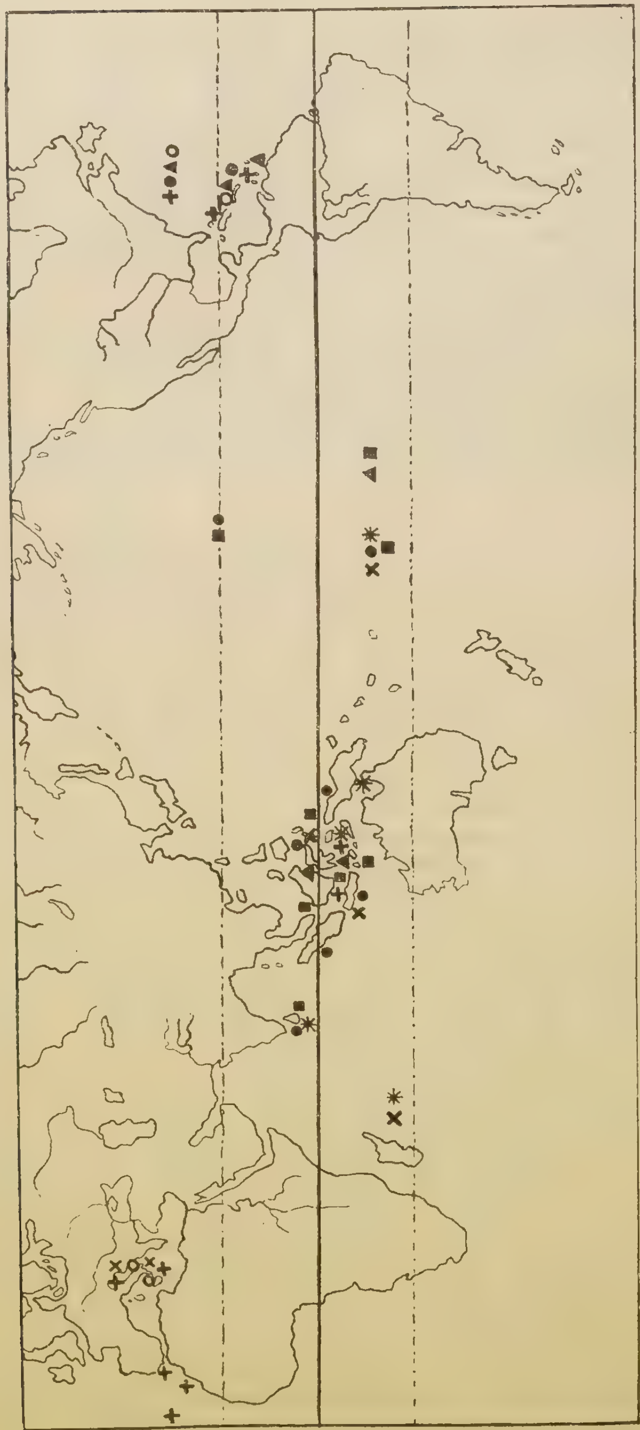

Fig. 5. The geographical distribution of *Valonia*.

● *V. pachynema*, Indian-Pacific, Atlantic.
+ *V. utricularis*, Indian-Pacific, Atlantic, Mediterranean.
▲ *V. ventricosa*, Indian-Pacific, Atlantic.
× *V. aegagropila*, Indian-Pacific, Mediterranean.
* *V. fastigiata*, Indian-Pacific.
■ *V. Forbesii*, Indian-Pacific.
○ *V. macrophysa*, Atlantic, Mediterranean.

West Indies, has entered the Carribbean Sea from the Mediterranean. To solve this problem satisfactorily is now impossible.

Dictyosphaeria (Fig. 6).

The remarkable genus *Dictyosphaeria* has about the same distribution as *Valonia* (compare Fig. 5 and Fig. 6). It is quite lacking, however, in the Mediterranean.

Common to the two Oceans is the widespread *D. favulosa* (AG.) DECSNE, which in the Atlantic is strictly limited to the West Indies and the Bermudas. It is not known from the Cape or from South Africa in general and in the Indian Ocean not further southwest than Mauritius. The species seems to have a continuous distribution in the Indian Ocean, enters the Red Sea rather far to the north (compare Fig. 6), is to be found in the whole Malayan Archipelago, and extends at least to the Hawai and Friendly Islands. On the western coast of Australia it is to be found as far south as Perth, thus a good distance south of the Tropic of Capricorn.

The remaining species of *Dictyosphaeria* have a considerably limited distribution, as far as is now known. *D. Versluysi* W. v. B. and *D. intermedia* W. v. B. are limited to the Malayan Archipelago and *D. Van Bosseae* BÖRGS. to the West Indies. The latter species seems to be very nearly related to *D. Versluysi*.

The present discontinuous distribution of the genus *Dictyosphaeria* is obvious and easily understood from the map (Fig. 6).

3. Dasycladaceae.

A fact of special interest is the distribution of the verticillate *Siphoneae*, the family *Dasycladaceae*, firstly because it is evidently of very great age. Owing to the fact that the majority of the *Dasycladaceae* are strongly calcified they have — contrary to most other Green Algae — been preserved as fossils and this so much the more easily as they are characterized by a gregarious mode of growth. Dasycladean Algae are known without doubt from the Carboniferous, Triassic and Jurassic times. The now existing genera can first be traced in Cretaceous times. Our knowledge of these plants from former ages is now very good on account of the comprehensive investigations of PIA.

The now existing representatives of the family *Dasycladaceae* are generally divided into three groups. According to PIA (1920) these are:

1. *Dasycladeae*, distinguished by their repeatedly branched whorls of branches, by the weak calcification of their tissue, and by the total lack of facetted cortex. To this group belong

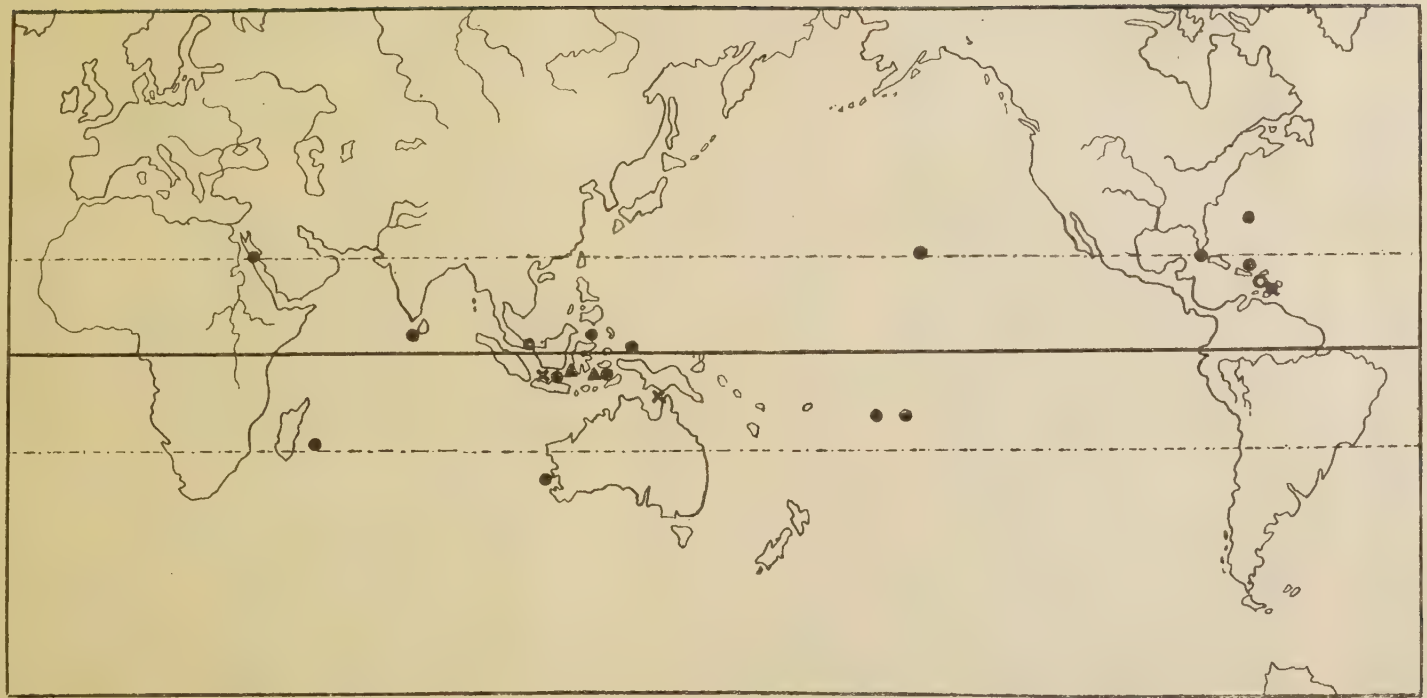

Fig. 6. The geographical distribution of *Dictyosphaeria.*

● *D. favulosa,* Indian-Pacific, Atlantic (West Indian). × *D. intermedia,* Indian-Pacific.
▲ *D. Versluysi,* Indian-Pacific. ○ *D. van Bosseae,* Atlantic, (West Indian).

A) *Batophora*, with many lateral gametangia on each branch and

B) *Dasycladus* and *Chlorocladus*, with only one seemingly terminal gametangium.

2. *Neomereae*, distinguished by their only once bifurcated branches, by their strong calcification, and by their more or less facetted cortex. To this group belong:

A) *Bornetella*, with many lateral gametangia on each branch and

B) *Neomeris* and *Cymopolia*, with only one seemingly terminal gametangium.

3. *Acetabularieae*, distinguished by the erect axis bearing at its summit a disc-like cap of radiating chambers, which produce the cysts containing the gametes; with the genera *Halicoryne*, *Chalmasia*, *Acetabularia*, and *Acicularia*.

The classification given above is not the most common one in the usual text-books; but as I have shown in another place (SVEDELIUS 1923, P. 461), it must be considered as the most natural one.

The genera are thus rather numerous; but only the *Acetabularieae*-group or to be exact the genus *Acetabularia* shows at present any greater abundance of species viz. about 15 species. The remaining genera have only one or a few species, a trait which is always characteristic of still surviving groups of great geological age.

Acetabularia.

The varying and critical genus *Acetabularia* has not yet been satisfactorily studied with regard to the definition of all its species and their geographical distribution. Therefore I have not found it possible to discuss its distribution in detail. It may, however, be pointed out that the distribution of the genus comprehends the West Indies — Canary Islands (and probably tropical West Africa) — the Mediterranean. In the Indian-Pacific Ocean it has a continuous distribution from South Africa in the west to the South American continent in the east. On the other hand it is not — so far as I know — found at the Cape, and the chance of its being found at the southern end of South America is of course still smaller. One species also occurs in the Mediterranean. The distribution is thus apparently discontinuous, and with regard to the immigration of the Mediterranean species the same holds good as was already said about the genera *Microdictyon*, *Anadyomene*, and *Valonia*.

Fig. 7. The geographical distribution of *Neomeris.*

× *N. annulata*, Indian-Pacific, Atlantic. + *N. van Bosseae*, Indian-Pacific. ⊙ *N. mucosa*, Atlantic.
● *N dumetosa*, Indian-Pacific, Atlantic. ▲ *N. stipitata*, Indian-Pacific. ○ *N. Cokeri*, Atlantic.

Neomeris (Fig. 7).

The genus *Neomeris* amongst the *Dasycladaceae* is more suitable for detailed comparisons regarding geographical distribution, as the species are relatively well known and well defined owing to the systematical works of HOWE and others.

The genus is a real tropical one (see Fig. 7) and numbers 6 species. None enters the Mediterranean.

The species which has the most extensive distribution is *N. annulata* DICKIE, which from the Atlantic is known only from the West Indies and the Bermudas. In the Indian-Pacific Ocean it is known from the east coast of Madagascar (Tamatave) and Mauritius in the west as far as from the coast of Chili (Cobija?) about the Tropic of Capricorn in the east. I have myself (SVEDELIUS, 1923) found it not far from the northern point of Ceylon at Paumben on the island of Ramesvaram in the Gulf of Manaar, at present the most northwesterly place in the Indian Ocean where it has been obtained.

Another species, *N. dumetosa*, LAMOUR., is also common to the two oceans. It has *e. g.* been found at the Lesser Antilles in the West Indies as well as at several localities in the Indo-Malayan Archipelago.

Besides these there are in the Indo-Malayan Archipelago two other species *N. van Bosseae* HOWE and *N. stipitata* HOWE, both, as far as is now known, with strictly limited distribution. In the West Indies, too, there are two more species, also with limited distribution, *N. Cokeri* HOWE and *N. mucosa* HOWE.

No species is found on the western and southern coasts of Africa nor at any other part of the African coasts. The map (Fig. 7) shows better than descriptions this apparently discontinuous distribution, which is the more remarkable as the species of this genus, owing to their calcification, cannot possibly float on the sea and thus be spread over great distances.

Cymopolia and Bornetella.

Amongst the *Dasycladaceae* the genus *Cymopolia* also has a discontinuous distribution. As lately as some 30 years ago only 2 species of *Cymopolia*, *C. barbata* (L.) HARV., and *C. mexicana* J. AG., were known, both from the tropical Atlantic. One of them, *C. barbata*, was also found at the Canaries and on the Atlantic coast of Spain (Cadiz). Since then a third species, *C. van Bossei* SOLMS (1893), has been found at several places in the Malayan Archipelago. The geographical distribution of this genus thus shows about the same type of discontinuity as *Neomeris*.

The genus *Bornetella*, which contains about 4—5 species and which belongs to the same systematic group as *Neomeris* and *Cymopolia* (comp. above P. 22), is on the other hand strictly limited to the Malayan Archipelago and the Pacific Islands, and no species is found in the Atlantic.

The geographical distribution of the other genera of *Dasycladaceae* — the group of *Dasycladeae* — viz. *Dasycladus*, *Chlorocladus*, and *Batophora*, will be discussed in a following chapter.

The genera of the family of *Dasycladaceae* now dealt with are all strictly tropical and — perhaps with the exception of *Acetabularia* — never met with at the southern points of the great Continents and thus all discontinuous with the exception of the strictly Indian Pacific genus *Bornetella*.

C. **Siphonales.**

In its geographical distribution the group *Siphonales* shows in many respects and especially in details a somewhat different type from the *Siphonocladiales*; but in the main we meet with the same discontinuity regarding most of the genera. An exception is, however, formed by the genus *Codium* amongst the *Codiaceae* and *Bryopsis* amongst the *Bryopsidaceae*. Both are varying, apparently eurythermal genera with many species, which both in the North and in the South go far outside the tropical zone, and of these many species are found at the Cape.

1. **Codiaceae.**

Codium.

The genus *Codium* has quite recently been monographed by O. CH. SCHMIDT (1923). From this it appears that amongst the approximately 30 species only two, *C. tomentosum* (HUDS.) STACKH. and *C. decorticatum* (WOODW.) HOWE (= *C. elongatum* AG.), are really cosmopolitan species and occur in nearly all oceans except the Arctic. Both occur at the Cape, so there is no discontinuity of their distribution in the two oceans. The whole genus and especially these two species are apparently very eurythermal. *Codium* contains also a great many endemic species with rather limited distribution, and the genus thus apparently shows an example of Algae which are still in active progress as regards the formation of new forms and species. In this respect it shows a remarkable difference from the above mentioned genera of *Siphonocladiales*.

In some respects, however, *Codium* also offers an example of discontinuous distribution. This concerns the group *Bursae* which contains about 4 species, some of which live in the Me-

diterranean, others in the Indian-Pacific Ocean. Their distribution will, however, be discussed later on (in chapter V, P. 51), when I shall also deal more thoroughly with the general geographical results of the paper of SCHMIDT.

The other tropical *Codiaceae*, however, show apparent discontinuity, but in contrast with the *Siphonocladiaceae*, the discontinuity of the *Codiaceae* is less evident in the geographical distribution of the species than in the distribution of the genus as a whole.

Many genera of the *Codiaceae* are very rich in species, especially *Aurainvillea*, *Udotea*, and *Halimeda*. There are not so many really common identical species of these genera in the two tropical oceans, but on the other hand, so many more »vicarious species», *i. e.* very alike, nearly related species, characterized only by small differences of which the one is confined to the Atlantic, the other to the Indian-Pacific. This whole group gives the impression of still developing new forms, in striking contrast to the group of *Siphonocladiales*, which with its many small genera, often very poor in species, seem rather to have been arrested in the evolution of new species.

Aurainvillea.

The genus *Aurainvillea* — at present rather well known owing to the monograph by A. and E. S. GEPP (1911) — contains, like *Codium*, rather many species — about 15 — but *Aurainvillea* is in contrast to *Codium* strikingly tropical. No species seems to go outside the real tropical zone. If *Codium* thus can be characterized as an eurythermal genus of *Codiaceae*, *Aurainvillea* on the contrary may be characterized as a stenothermal one.

Some of the species of *Aurainvillea* have a very extensive range of distribution, others seem to be strictly local, but no species is common to the Atlantic and the Indian-Pacific Ocean.

The very varying *A. lacerata* J. AG. has certainly the most extensive distribution of all Aurainvilleas. It ranges from the East Indies in the west to the Pacific Islands in the east. In the western parts of the Indian Ocean *A. lacerata* is replaced by *A. amadelpha* GEPP. These two species are very nearly related to *A. sordida* MURRAY & BOODLE and *A. asarifolia* BÖRGS. respectively, which both occur in the West Indies. To the same group belong the more local *A. pacifica* A. & E. S. GEPP from the eastern parts of the Pacific Ocean and the nearly related *A. Gardineri* A. & E. S. GEPP in the western Indian Ocean. The last mentioned finds its counterpart in the West Indies in the rather common *A. nigricans* DCSNE, to which some other West Indian species are nearly allied viz. *A. Rawsonii* HOWE,

A. Mazei, MURRAY & BOODLE, *A. Elliottii* A. & E. S. GEPP, and others.

One species, *A. canariensis* A. & E. S. GEPP, goes in the Atlantic as far east as to the Canaries. This is the only species of *Aurainvillea* found near the west coast of Africa.

One more species with extensive distribution is known from the East Indies viz. *A. erecta* (BERKL.) GEPP, which extends from the East Indies to New Guinea. Nearly related to this species but with more local distribution are: *A. obscura* J. AG. (Marian Islands), *A. Ridleyi* A. & E. S. GEPP (Christmas Island), and *A. clavatiramea* A. & E. S. GEPP (Victoria, South Australia).

No species is found at South Africa.

Aurainvillea thus shows a fine example of a genus with couples of vicarious species in the two tropical oceans. The distribution of the genus is now sharply divided into two separate areas, and neither at the Cape nor at Tierra del Fuego are any Aurainvilleas to be found. But on the other hand, these areas have no species in common. Many quite local species occur in both of the two separate areas, which shows that a rather active evolution of new forms has gone on even after the separation of the two areas.

Rhipilia.

The genus *Rhipilia*, established by KÜTZING (1858) and formerly united with the *Aurainvillea*, shows principially the same distribution as this genus. It contains, however, only a few (3) species, of which *Rh. tomentosa* KÜTZ. is rather extensively distributed in the West Indies and is also found at the Canaries. Another species, *Rh. tenaculosa* GEPP, is also found in the Atlantic (Pernambuco), while the third, *Rh. orientalis* GEPP, is found at the Borneo-bank in the Malayan Archipelago. This distribution of the genus is very remarkable and apparently discontinuous.

Cladocephalus (Fig. 10).

The curious distribution of the genus *Cladocephalus* will be discussed later on (chapt. III, P. 44) in connection with the genus *Chamaedoris* of the family of *Siphonocladiaceae*. These two genera have in many respects a similar distribution of a quite singular type.

Penicillus.

The peculiar genus *Penicillus* is mostly West Indian with very few species in other seas.

Many of the species, such as *P. capitatus* LAM. and *P. pyriformis* GEPP, belong to the most characteristic marine Algae of the tropical West Indies and seem to appear gregariously. On the other hand, the genus seems in the Atlantic to be confined

to the West Indies and the Bermudas, and no *Penicillus* has as yet been found on the African coasts, neither in the Atlantic nor the Indian Ocean.

It is, however, remarkable that a *Penicillus* (of the subgenus *Espera*) occurs in the Mediterranean on the south coasts of France viz. *P. mediterraneus* Thuret. To the same systematic group as *P. mediterraneus* belong — curiously enough — the two other species of *Penicillus* which are found outside the Atlantic, namely, *P. nodulosus* Blainv., which is known from the Moluccean Islands and from northern and western Australia, and *P. Sibogae* Gepp from Timor. This distribution is very remarkable and will be discussed in the next chapter.

The discontinuity of the distribution of *Penicillus* is apparent with one centre in the West Indies and another in the Indo-Malayan Archipelago and Australia and, finally, one species in the Mediterranean. In any case there is no connection via the Cape and still less over Tierra del Fuego.

Udotea (Fig. 8).

Udotea is, as to the number of species, one of the richest genera amongst the *Codiaceae*. Of about 15 species, which are practically all to be found in the tropical zone, one only is known to be common to the Atlantic and the Indian-Pacific Ocean viz. *U. flabellum* Howe, which is commonly distributed in the West Indies and the Bermudas, but which is not found from the Atlantic coast of Africa (comp. Fig. 8). It is not known from the Cape nor from the eastern coast of Africa but from the Red Sea, the Indian Ocean (East Indies and Ceylon), the Indo-Malayan Archipelago, and the Pacific Islands at least as far as to the Friendly Islands.

The other species occur in practically equal numbers in the West Indies and the Indian-Pacific Ocean. Many species in one of these areas correspond to some very nearly allied species in the other, just as was the case regarding the genus *Aurainvillea* already mentioned above. Such couples of vicarious species are:

Indian-Pacific:		West Indian:
U. argentea Zan.	—	*U. occidentalis* Gepp
U. explanata Gepp	—	*U. cyathiformis* Dcsne
U. papillosa Gepp	—	*U. verticillosa* Gepp *U. Wilsoni* Gepp et Howe
U. palmetta Dcsne	—	*U. spinulosa* Howe

Those in the first column are Indian-Pacific species, those in the second, West Indian.

U. argentea has a wide range from the Red Sea to the eastern

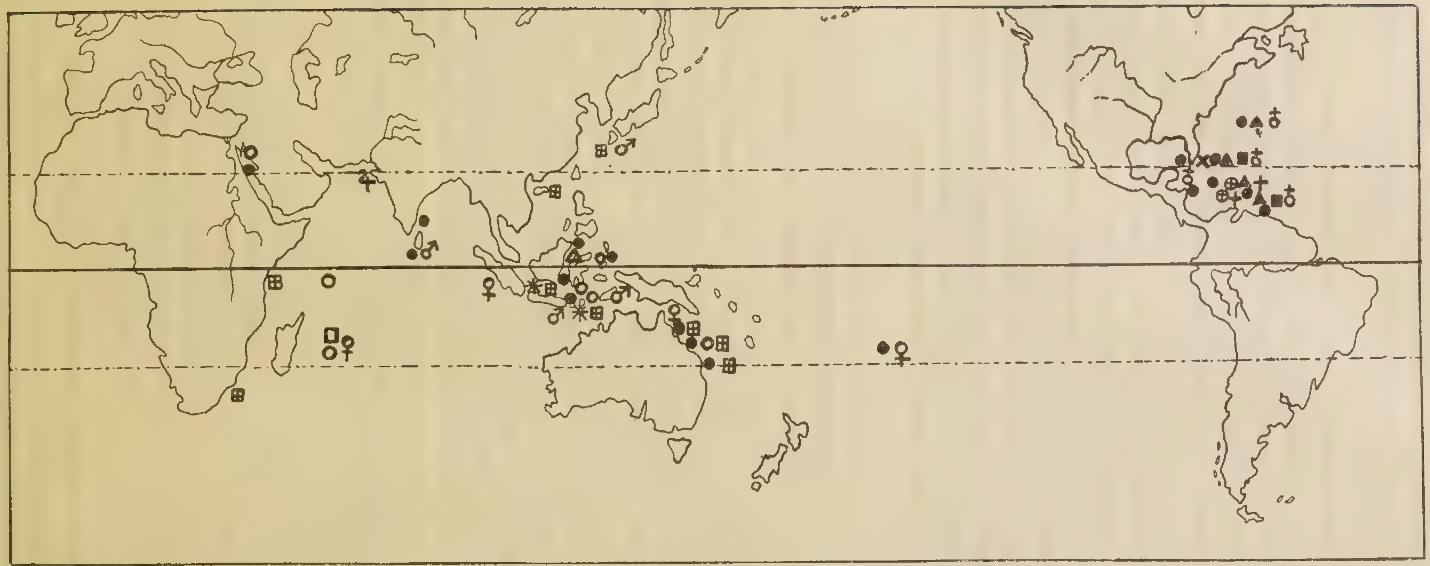

Fig. 8. The geographical distribution of *Udotea*.

● *U. flabellum*, Indian-Pacific, Atlantic.
⊞ *U. orientalis*, Indian-Pacific.
♀ *U. glaucescens*, Indian-Pacific.
♂ *U. javensis*, Indian-Pacific.
♃ *U. indica*, Indian-Pacific.
♁ *U. conglutinata*, Atlantic.

Vicarious species:

○ *U. argentea*, Indian-Pacific — ⊕ *U. occidentalis*, Atlantic.
△ *U. explanata*, Indian-Pacific — ▲ *U. cyathiformis*, Atlantic.
✳ *U. papillosa*, Indian-Pacific — + *U. verticillosa*, Atlantic. × *U. Wilsoni*, Atlantic.
◘ *U. palmetta*, Indian-Pacific — ■ *U. spinulosa*, Atlantic.

coast of tropical Australia, whereas *U. occidentalis* is from the former Danish West Indies.

U. explanata is quite local in the Malayan Archipelago (Celebes), but the similar species *U. cyathiformis* is widely distributed in the West Indies. These two species are so closely allied that one can be in doubt if they are not the same species. It is also very characteristic that Mrs GEPP (1911, P. 121) says that she would perhaps not have hesitated to identify the Alga from Celebes with that from the West Indies if the places of their discovery were not so widely separated.

U. papillosa is from the Malayan Archipelago, and the nearly allied *U. verticillosa* and *U. Wilsoni* are from the former Danish West Indies and the Bahama Islands respectively.

U. palmetta is found at the Mascaren Islands (Mauritius), and the nearly allied *U. spinulosa* is from the West Indies.

Except for the species found in the Bermudas (*U. flabellum*, *cyathiformis*, and *conglutinata*) no *Udotea* in the Atlantic passes beyond the tropics.

In the Indian-Pacific Ocean one species goes beyond the tropics both in the north and in the south, viz. *U. orientalis* GEPP, which is known as far southwest as off Port Natal (Durban) in Africa and also as far northeast as southern Japan. The same northern latitude is also reached by another species, *U. javensis* GEPP, found also in the Malayan Archipelago.

The discontinuous distribution of the genus *Udotea* is clearly shown on the map (Fig. 8), and it is particularly striking that all the Atlantic species are concentrated in the West Indies. Not a single one has hitherto been found from the west coast of Africa.

Halimeda (Fig. 9).

The genus *Halimeda*, which also belongs to the family *Codiaceae* and is also rich in species, is very characteristic of the tropical coral reefs. The species are always incrustated with carbonate of lime, appear gregariously, and often form a special feature of the coral reefs. The distribution is in the main about the same as that of *Udotea* (comp. Fig. 8 and Fig. 9). One species, however, *H. Tuna*, is also rather common in the Mediterranean.

H. Opuntia (L.) LAMX. seems to be the most common of all the species in the tropical Oceans from the Red Sea in the west, through the Indian-Pacific Ocean as far as to Hawai (MAC CAUGHEY, 1918) and Easter Island (BÖRGESEN, 1924). In the Atlantic it is confined to the West Indies and is not yet reported from the African coast of the Atlantic nor from the Cape. This is very remarkable as such a characteristic and

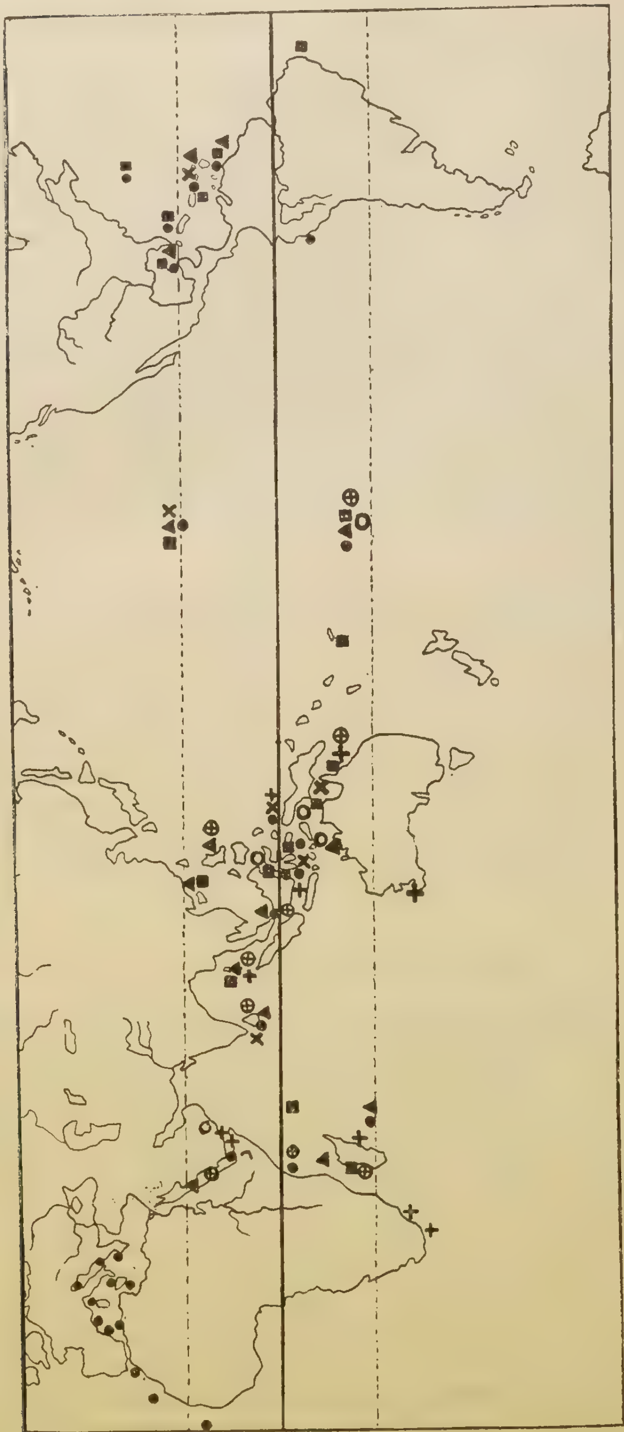

Fig. 9. The geographical distribution of *Halimeda.*

● *H. Tuna*, Indian-Pacific, Atlantic.
▲ *H. Opuntia*, Indian-Pacific, Atlantic.
× *H. gracilis*, Indian-Pacific, Atlantic.
■ *H. incrassata*, Indian-Pacific, Atlantic.
+ *H. cuneata*, Indian-Pacific.
○ *H. macrophysa*, Indian-Pacific.
⊕ *H. macroloba*, Indian-Pacific.

conspicuous Alga as *H. Opuntia* would scarcely have escaped observation if it really occurred there.

H. Tuna (ELL. et SOL.) LAMX. has a very wide range from the whole of the West Indies to the western coast of Africa (Tangier — the Canaries — Cape Verde Islands). It is also known from many places in the western part of the Mediterranean. It also occurs in the Red Sea and in the Indian-Pacific Ocean from Zanzibar and Mauritius in the west through the Malayan Archipelago as far as to the western coast of South America (Callao). It also occurs in Hawai (MAC CAUGHEY, 1918), whereas it is not found on the South African coasts.

Species common to the Atlantic and the Indian-Pacific Ocean are further:

H. gracilis HARV., which in the West Indies seems to be somewhat rare, and which in the Indian Ocean is not found farther west than Ceylon but in the Pacific goes at least as far as to Hawai; and

H. incrassata (ELL. et SOL.) LAMX., which has the same distribution as the previous species. It seems, however, to be rather more common in the West Indies than *H. gracilis* and is also known from Pernambuco in Brazil. In the Indian Ocean it is not known farther west than the Seychelle Islands and Madagascar.

Besides these species in common there are, further, about 3 species (*H. cuneata* HER., *macrophysa* ASK., and *macroloba* DCSNE) in the Indian-Pacific Ocean, whereas on the other hand no species is found only occurring in and limited to the West Indies. All the West Indian species are thus found in the Indian-Pacific Ocean.

H. cuneata has a remarkable distribution. It belongs to the Algae which are common to South Australia and South Africa and at both continents — in Africa at Port Elizabeth and in Australia at Freemantle — it goes farther south than any other *Halimeda*, far outside the Tropic of Capricorn.

The other strictly Indian-Pacific species do not go outside the tropical zone. *H. macrophysa* is Indo-Malayan and extends at least to the Friendly Islands. *H. macroloba* moreover goes a little further west and occurs in the Red Sea and on the Eastern coast of Africa.

Regarding the distribution of the genus *Halimeda* it may be summarily characterized as having its centre of development of new forms in the Indian-Pacific Ocean in contrast to *Aurainvillea*, *Udotea*, and especially *Penicillus*, which in this respect are more West Indian.

Only two species of *Halimeda* go outside the tropical zone viz. *H. Tuna* in the Mediterranean and *H. cuneata* in the Indian

Ocean. It is to be noticed that according to E. S. Barton (Mrs. Gepp), who has written a monograph on the genus (1901), these two species are very closely allied. Thus the Mediterranean species has its nearest related species in the Indian Ocean. This distribution will, however, be more closely discussed in a following chapter (see P. 56!).

2. **Caulerpaceae.**

Caulerpa.

The distribution of the genus *Caulerpa* which at one time gave me the clue to the right explanation of the remarkable resemblance between the marine Algae in the West Indian and the Indian-Pacific waters, need not again be discussed in detail, as I have already given an account of it in two publications viz. Bot. Notiser (Svedelius, 1906, *a*) and Ceylon Mar. Biol. Reports (Svedelius, 1906, *b*).

The geographical distribution of the Caulerpas shows great resemblance to that of *Halimeda*. The two genera seem to have their centre of distribution located in the Indian-Pacific Ocean. There most of the species are found; but whereas the genus *Halimeda* does not show one single species characteristic of the West Indies, the genus *Caulerpa*, on the other hand, has at any rate some West Indian species which do not occur in the Indian-Pacific Ocean. Thus for instance Börgesen (1914) found in the former Danish West Indies 2 species of *Caulerpa* which are lacking in the Indian-Pacific Ocean viz. *C. prolifera* (Forsk.) Lamx., which is also Mediterranean, and *C. Ashmeadi* Harv. which is exclusively West Indian. In South African waters there is only one species of *Halimeda* — *H. cuneata* — whereas of *Caulerpa* there are perhaps a few; but the Indian species are only found on the eastern coast which is washed by the warm tropical Mozambique-current.

At the southern end of South America, for instance, there is no *Caulerpa*; nor are there any *Halimeda* or other tropical Siphonean Algae.

The genus *Caulerpa* — considered as a whole — has then, perhaps, a nearly continuous distribution from the Atlantic to the Indian-Pacific Ocean, except as regards the species for which South Africa constitutes a sort of barrier which is not passed either by the Atlantic or by the Indian-Pacific species. The discontinuity in this respect is thus apparent.

2. **Phaeophyceae.**

A comparison between the *Phaeophyceae* in the tropical Atlantic and the Indian-Pacific Ocean from the point of view

of showing the plant-geographical connection is not so easily made as between some groups of the *Chlorophyceae*. This depends partly upon the fact that the *Phaeophyceae* in general do not play the same dominant part in the tropical marine flora as in the flora of more temperate seas. The material for comparison is in other words much more scarce.

The *Phaeophyceae* of the former Danish West Indies are e. g. according to BÖRGESEN only half as numerous as the *Chlorophyceae* or 45 against 90. Of these 45 species of *Phaeophyceae* only 18 are found in the Indian-Pacific Ocean. Thus, for instance, those numerous small and well defined genera with relatively few species — so characteristic of the tropical *Chlorophyceae* — are quite lacking. The great genera rich in species, as for instance, *Sargassum*, *Ectocarpus*, *Dictyota*, *Dictyopteris* (= *Haliseris*), and others, are mostly critical genera, uninvestigated and still waiting for their monographers. Therefore, they are not at present suitable for comparison. In treating of the group of the *Phaeophyceae* I am thus compelled to be brief.

That the *Ectocarpaceae* at present are not suitable for comparisons of this kind is apparent to everyone who has been working at determinations of these Algae. The uncertainty with regard to the definition of the species is too great for any conclusions in this respect to be drawn concerning these plants.

The case is pretty much the same regarding the *Sphacelariaceae*. The two West Indian species of *Sphacelaria* which are noticed by BÖRGESEN (1914) from the former Danish West Indies have certainly a wide range also in the Indian-Pacific Ocean; but as they very probably also occur on the coasts of South Africa, their distribution does not show any discontinuity.

The same is most probably the case with several other *Phaeophyceae* common to the tropical Atlantic and the Indian-Pacific Ocean as, for instance, *Colpomenia sinuosa*, *Hydroclathrus cancellatus*, *Zonaria lobata*, and others.

Regarding the *Phaeophyceae* the most remarkable fact is that the genus *Sargassum*, though richest in species amongst all the tropical genera, does not show any species certainly common to the tropical Atlantic and the Indian-Pacific Ocean. As a whole, the West Indies seem to be very poor in Sargassa. BÖRGESEN does not mention more than 4 species for the Danish West Indies, which is very little, considering that about 150 so-called good species are known. None of these 4 species is known outside the Atlantic.

Of the genus *Padina*, so common in tropical seas, no species common to the two great tropical oceans are known; but West Indian species are very nearly related to some others in the In-

dian-Pacific Ocean, as for instance the West Indian *P. gymnospora* (KÜTZ.) VICKERS to the East Indian *P. australis* HAUCK.

The case appears to be somewhat different regarding the varying genus *Dictyota*. BÖRGESEN reports for the Danish West Indies 8 species, of which 3—4 also occur in the Indian-Pacific Ocean. This, for instance, is the case with *D. Bartayresiana* LAMX., *pardalis* KÜTZ., and *crenulata* J. AG. Whereas the former two species are found in the Indo-Malayan Archipelago, the latter, *D. crenulata*, occurs on the Pacific coast of Mexico. In the West Indies there are still about half a dozen species, which otherwise are not known from any ocean but the Atlantic and perhaps the Mediterranean. Most other species — about 20—30 — belong to the Indian-Pacific Ocean.

An examination of the *Phaeophyceae* (incl. *Dictyotales*) shows, then, that very few species are common to the two Oceans and fewer still have a discontinuous distribution, which is probably due to the fact that the *Phaeophyceae* are on the whole of younger date than the genera of the *Chlorophyceae* treated above.

3. **Rhodophyceae.**

BÖRGESEN (1920, P. 492) has shown, in his work on the Algae of the former Danish West Indies repeatedly quoted above, that of all the known *Rhodophyceae* (192) only 47, or about one-fourth, are found in the Indian-Pacific Ocean. Compared with the *Chlorophyceae* — 90 in all, as many as 46 of which are found in the Indian-Pacific Ocean — this number is surprisingly small and may seem at first sight to contradict the conclusions regarding the geographical relations of the two floras which were drawn from the distribution of the *Chlorophyceae*. BÖRGESEN, however, has concluded from these facts — in my opinion quite correctly — that the greater part of the *Rhodophyceae* are of a young date, i. e. a lively formation of species has taken place in the West Indies after the separation from the Indian-Pacific Ocean. He has not elucidated this matter thoroughly. It seems to me, however, to be of such importance that it ought to be studied, even if such a comparison must always be rather uncertain, owing to our present lack of knowledge of the real distribution of the *Rhodophyceae* in the Indian-Pacific Ocean.

Regarding the *Rhodophyceae* a comparison can only be made concerning a rather limited number of genera viz. such in particular as have recently been monographically dealt with.

1. **Helminthocladiaceae.**

Liagora.

Within the family of *Helminthocladiaceae* the genus *Liagora* may be briefly mentioned.

BÖRGESEN (1915) found 6 species of *Liagora* in the Danish West Indies, and Mme WEBER VAN BOSSE (1921) found 6 species in the Dutch East Indies. Of these species 3 are common viz. *L. elongata* ZAN., *L. valida* HARV. and *L. pulverulenta* C. AG.

No species is known from the Cape. In any case BARTON (1893) does not mention any from that region. Thus, the distribution of the genus is discontinuous and seems in the main to correspond to that of the members of the *Siphonocladiaceae* treated above. The species in common seem chiefly to belong to the Indian Ocean. *L. elongata* and *pulverulenta* also enter the Red Sea, while *L. valida* is not known farther west than Madagascar.

Scinaia.

The genus *Scinaia* has lately been the object of particular systematic investigations by SETCHELL (1914), the result of which has been to establish a new genus *Pseudoscinaia* and several new species.

For instance, many forms of the genus *Scinaia* from different parts of the world, earlier wrongly determined as *Sc.* »*furcellata*», have proved to be new species. The real *Sc. furcellata* (TURN.) BIV. has a rather limited distribution, though it was only a few years ago regarded as a cosmopolite.

According to SETCHELL's revision the genus *Scinaia* contains 11 species, only 2 of which occur in the Atlantic. The rest belong to the Indian-Pacific Ocean, whilst one species also occurs at the Cape. The majority belong to the northern hemisphere. No species is common to the Atlantic and the Indian-Pacific Ocean.

It is remarkable, however, that the Atlantic species are not most nearly allied to the species from the Cape. The North Atlantic and Mediterranean *Sc. furcellata* belongs to the same group as the Pacific *Sc. Johnstoniae* SETCH. from California and *Sc. japonica* SETCH. from Japan. The other Atlantic species, the tropical *Sc. complanata* (COLL.) COTT., belongs to the same group as *Sc. latifrons* HOWE and *Sc. Cottonii* SETCH., of which the former occurs in South California, the latter in Japan. The species from the Cape has its most nearly related species at Ceylon, Philippine Islands, Hawai, and California.

If we suppose with MURRAY that the connection between the two centres of distribution of Algae in the great oceans was via the Cape, it seems curious that the Atlantic species are not all the nearest allied to the species from the Cape. If, on the other hand, we suppose that the connection was over the isthmus of Panama, the fact that the Atlantic species have their most nearly related species at about the same latitude in the

Pacific will be more easily explained. The *Scinaia*-group has evidently had its centre of evolution in the Pacific, especially in the northern part, judging from the fact that no less than half of all known species belong there. From these the species have spread partly southward and westward across the Indian Ocean to Australia and the Cape, partly eastward into the Atlantic through the open connection to the Caribbean Sea.

Whether *Sc. furcellata* in the Mediterranean really immigrated there from the west viz. from the Atlantic or perhaps from the east viz. from the Indian Ocean by the open channels between the Atlantic and the Pacific in tertiary times is, of course, now impossible to decide. This problem will be discussed in a following chapter.

Gloiophlaea.

On the hypothesis of a connection over Panama we get the natural explanation of the geographical distribution of the genus *Gloiophlaea* J. AG., which is most nearly related to *Scinaia*.

According to SETCHELL, this genus seems to have its centre of distribution in the southern Pacific, whence it immigrated into the northern Pacific. At present 2 species are known from the northern Pacific viz. *G. Okamurai* SETCH. from Japan and *G. confusa* SETCH. from the western coast of North America; 2 species are known from the southern Pacific viz. *G. scinaioides* J. AG. from South Australia—New Zealand and *G. undulata* (MONT.) SETCH. from the western coast of South America. Besides these, one species is known from the Cape. This species, according to SETCHELL, comes next to the Californian *G. confusa* SETCH.

But there is still another species, *G. Halliae* SETCH. from Florida, the only species known from the Atlantic. After having made his supposition as to the probable Pacific origin of the genus — supported by the analogy in distribution of the *Lessonia*—*Ecklonia*-group amongst the *Laminariaceae* — SETCHELL comes to this West Indian *Gloiophlaea*, the geographical distribution of which seems to have afforded him difficulties, for he says: »The occurrence of a *Gloiophlaea* in the North Atlantic (Florida coast) seems, from this point of view, anomalous» (SETCHELL, 1914, P. 134). On the supposition of an interoceanic connection and immigration over the Panama Isthmus when the Carribbean Sea was a great bay of the Pacific, this distribution, however, is not at all »anomalous» but rather natural and simple, and the analogy in distribution with *Scinaia* and several other types seems quite clear. Also, according to SETCHELL, this West Indian species *G. Halliae* is most closely related to the Pacific *G. Okamurai*.

Galaxaura.

The genus *Galaxaura*, which belongs to the same family as *Scinaia*, was some years ago the object of detailed monographical treatment by KJELLMAN (1900), in which the geographical distribution of the genus was discussed. Unfortunately the definition of the species is in many respects very uncertain because KJELLMAN probably has described as different species tetrasporic and sexual individuals which, according to later discoveries, belong together i. e. are generations of one and the same species.

HOWE (1917, 1918) has namely since the publication of KJELLMAN's work made the remarkable discovery that in the genus *Galaxaura* sexual and tetrasporic individuals sometimes differ not only in their different organs of propagation but also in the different anatomical structure of the cortex. At the time when KJELLMAN wrote his *Galaxaura*-monograph this was something quite unknown regarding other genera too. KJELLMAN then established two new groups of the genus, *Rhodura* and *Microthoë*, based particularly upon anatomical characteristics of the cortex. To the former KJELLMAN referred some species of which only tetrasporic individuals were known and to the latter some of which only sexual individuals were known. Now, after the discovery of HOWE it seems more than probable that these two groups of species of KJELLMAN ought to be united. The result of this, however, would be that no certain conclusions regarding geographical distribution can be drawn from this monograph. Some geographical results may, however, be obtained therefrom.

As the main centra of distribution of *Galaxaura* KJELLMAN mentions the following ocean areas: in the Atlantic the West Indies; in the Pacific Japan, the eastern and southern coasts of Australia; and in the Indian Ocean the south-eastern coast of Africa. Now it will be observed that neither the *Rhodura* nor the *Microthoë* group is represented in the Indian Ocean, but occurs with about the same number of species in the Pacific and the West Indies. Consequently, these two groups of *Galaxaura*, which in all probability form only one single natural group, occur in the West Indies and in the Pacific but not in the Indian Ocean nor for that matter on the coasts of South Africa. This type of distribution is apparently the same as we have already become acquainted with in the species of *Scinaia*, and it receives its natural explanation by the supposed connection across Panama as was described above.

Now it is to be noticed that the number of species common to the Atlantic and the Indian-Pacific Ocean is not very great. Thus for instance WEBER v. BOSSE (1921) has found 17 species of *Galaxaura* in the Dutch East Indies, of which only 3(—4) also

occur in the West Indies. The Galaxauras are, however, very varying and rich in forms, partly critical; so for the reasons mentioned above (P. 12, 36) it is not to be expected that the conformity of species should be very great. The distribution of the groups clearly shows that there must once have been a geographical connection between the oceans, which explains the resemblance between the species in the Pacific and the Atlantic (West Indies). A supposed connection via the Cape does not explain the present distribution.

2. Squamariaceae.

The family of *Squamariaceae* is very richly represented in the tropics, but the definition of the species is very uncertain, for which reason the family is not at present suitable for plant-geographical comparisons.

It is further quite evident that the West Indies and the Indian-Pacific Oceans have not many species in common. Mme WEBER V. BOSSE (1921) found during the Siboga Expedition no less than 25 species from the Dutch East Indies; but more than 20 of these are as yet only known from the Indian Ocean and adjacent seas. This indicates a very lively formation of species now going on, and such genera do not supply any arguments for previous connections between the Atlantic and the Indian-Pacific Oceans.

3. Corallinaceae.

What has just been said about the *Squamariaceae* holds good also for the *Corallinaceae*. This very varying family, the species of which are among the most characteristic Algae of the tropical reefs, is apparently represented by quite different species in the two great Oceans. The tropical *Corallinaceae* in the West Indies seem also to have a very limited distribution. Of about 20 species which BÖRGESEN (1917, P. 149) found in the Danish West Indies only 3 occur on the Atlantic coasts of both Europe and Africa. Amongst these *Melobesia farinosa* LAMX. seems to be cosmopolitan. On the other hand, Mme PAUL LEMOINE (1917), who has worked out the *Melobesieae* in BÖRGESEN's work, points out the very striking fact that the *Melobesieae* of the Antilles show a remarkably large number of species much like or vicarious with species from the Mediterranean and the Indian-Pacific Ocean.

If we compare these statements with the results of the Siboga Expedition regarding this family — of about 32 species found in the Dutch East Indies only 3—4 are known in the Atlantic and 1 in the Mediterranean — it is evident that the *Melobesieae*

are in an stage of active evolution, and consequently different parts of the Oceans are characterized by quite different species. Thus evidently the Mediterranean, the West Indies, the Indian and the Pacific Ocean are all separate centres of formation of species.

4. Ceramiaceae.

Concerning the great family of *Ceramiaceae* the West Indies and the Indian-Pacific Ocean have very few species in common. For instance, there is in the Danish West Indies according to BÖRGESEN amongst the following genera of *Ceramiaceae* — viz. *Spermothamnium*, *Griffithsia*, *Callithamnion*, *Seirospora*, *Antithamnium*, and *Crouania* — not a single species which is also found in the Indian-Pacific Ocean. And the species which are really found in common are such as *Centroceras clavulatum* (C. AG.) MONT. or other really cosmopolitan species with a very wide range in all seas.

For the family of *Ceramiaceae*, then, as well as for the *Corallinaceae*, the great oceans are separated centres of origin of species. The family of *Ceramiaceae* also presents just the characteristics which are so typical of groups of plants in lively formation of species: great genera with very many critical species.

5. Rhodomelaceae.

As is the case with the *Ceramiaceae*, the family of *Rhodomelaceae* shows some great genera with many species, few of which occur in both oceans. But in this family we also meet with small, well defined genera with few species, and these genera just like the *Siphonocladiaceae* sometimes show very clear discontinuous distribution.

Of the great critical genera of the *Rhodomelaceae*, the Atlantic and the Indian-Pacific Ocean have very few species in common with discontinuous distribution, but several species in common with continuous distribution over the two oceans.

Genera with very few species in common are for instance:

Laurencia (of the 6 species found in the Danish West Indies only 1 is also found in the Indian-Pacific Ocean);

Chondria (of 4 species in the Danish West Indies possibly 1 in the Pacific);

Polysiphonia (of about 6 species from the Danish West Indies only 1 found in the Indian-Pacific Ocean).

Other genera of this family, as for instance *Bryothamnium*, *Herposiphonia*, *Lophosiphonia*, and *Dasya* are in the West Indies represented by exclusively Atlantic species.

Dictyurus.

As a very instructive example of a genus of *Rhodomelaceae* with but few species of which one is West Indian and the other Indian-Pacific, the genus *Dictyurus* may be mentioned.

This wonderfully elegant Alga with its very complicated, delicate structure — certainly one of the most beautiful of all Red Algae — forms a very well defined and rather isolated type of organization in the family. FALKENBERG (1901) in his great monograph on the *Rhodomelaceae* places the genus in the genealogy (l. c. P. 700) as a special branch, which has differentiated very early in the evolution of the family and followed its own line of development. Of this very remarkable genus only 2 species are now known viz. *D. purpurascens* BORY from the Indian Ocean and *D. occidentalis* J. AG. from the West Indies. The Atlantic species has evidently a very limited distribution, that is to say, it is strictly confined to the West Indies and is e. g. not known from Bermuda, which otherwise harbours so many West Indian Algae, nor from the coast of Africa. The Indian species *D. purpurascens* is not known farther west in the Indian Ocean than from Mauritius: it grows at Ceylon and as far east as at Tanah Djampea (south of Celebes) in the Malayan Archipelago (WEBER VAN BOSSE, 1923, P. 381). On the other hand it does not occur at the Cape nor in the Pacific Ocean; the distribution of the genus, then, is evidently discontinuous, and in this respect it shows some analogy to the Dasycladean genus *Neomeris* treated above (P. 25).

The family of *Rhodomelaceae* is thus an instructive example of the law I have already dwelt upon that small, well defined, evidently very old genera have very nearly allied species in the tropical Atlantic and the Indian-Pacific Ocean, whereas the great critical genera show greater differences, which evidently proves that these genera have followed their own lines of development in the different oceans.

Amongst the *Rhodomelaceae*, too, there are naturally examples of the cosmopolitan types which occur in all warmer seas and which have an evenly continuous distribution, such as *Digenea simplex*, *Bostrychia tenella*, and others.

6. Delesseriaceae.

The family of *Delesseriaceae* does not seem to play the same dominant part in the tropical seas as in the temperate ones. The family does not in the tropics exhibit any genera with many species.

Some of the Algae belonging to this family, as e. g. *Taenioma perpusillum* J. AG. and *Caloglossa Leprieurii* (MONT.) J. AG., are strikingly cosmopolitan with continuous distribution via the Cape. Other genera, however, show examples of the above mentioned discontinuity. This is the case with the characteristic genus *Martensia*.

Martensia.

The genus *Martensia* (SVEDELIUS, 1908) has a very fine and delicate structure, in some ways analogous to that of *Dictyurus* amongst the *Rhodomelaceae*. At present about half a dozen species are known, all with the exception of one, *M. Pavonia* J. AG., from the Indian-Pacific Ocean. One species is known as far west as south-eastern Africa viz. *M. elegans* HER. from Port Natal, a species which has its main distribution off South Australia. Near it stands the Ceylon species *M. fragilis* HARV. The West Indian *M. Pavonia*, which is strictly confined to the West Indies, is on the other hand most nearly related to the Australian *M. denticulata* HARV.; these two species form a distinct little group within the genus.

Thus we see here a repeated example of what has already often been pointed out: a small, very distinct genus with its main distribution in the Indian-Pacific Ocean, where many species belong, has one species in the West Indies nearly related to an Australian or Indian species but not to the species from the Cape, also localized to the eastern coast of Africa washed by the warm Mozambique current from the Indian Ocean.

The remaining families of the *Rhodophyceae* do not show anything principially new as regards the problem here treated beyond what has already been mentioned. We find, then, a number of cosmopolitan species with continuous distribution as for instance *Catenella Opuntia* (G. et W.) GREV., *Gracilaria confervoides* (L.) GREV., *Hypnea musciformis* (WULF.) LAMX., *Hypnea cervicornis* J. AG., and others.

The genera with many species amongst these families viz. *Gracilaria*, *Chrysymenia* show very few or no species common to the Atlantic and the Indian-Pacific Ocean. Of the ten species of *Gracilaria* found in the West Indies only two, for instance, are found outside the Atlantic, and of these two, one is the cosmopolitan *Gr. confervoides*.

Of about 6 species of *Chrysymenia* found in the West Indies none is known from the Indian-Pacific Ocean, which, however, harbours several species of the genus. None is known from the Cape. Thus the discontinuity of distribution is apparent.

III. Discontinuous species common to the Atlantic and the Indian Ocean, which in the Indian Ocean have only a western distribution.

The two genera *Chamaedoris* and *Cladocephalus* have a rather remarkable distribution, in many respects diverging from that of the other discontinuous Algae.

Chamaedoris is a monotypical genus amongst the *Siphonocladiaceae*, and *Cladocephalus* is a small genus with only 3 species which belong to the *Codiaceae*. What is remarkable concerning their distribution is not that they are discontinuous i. e. lacking on the southwestern coast of Africa like so many other discontinuous tropical Algae, but that they do not at all occur in the Pacific and only in the western parts of the Indian Ocean. In this respect they represent a quite special type of distribution, which is the reason why they will here be treated separately.

Chamaedoris (Fig. 10).

Chamaedoris with its simple species *Ch. Peniculum* (SOL.) KUNTZE (Syn. *Ch. annulata* (LAM.) MONT.) forms amongst the *Siphonocladiaceae* a type of organization which in its appearance in some ways resembles the genus *Penicillus* amongst the *Codiaceae*. The main stem, for instance, has in the summit a dense mass of filaments just like a brush or mop. This gives the plant a very curious appearance.

This Alga has a rather wide range in the West Indies (Fig. 10), but seems in the Atlantic not to go as far north as to the Bermudas, where otherwise so many West Indian tropical Algae occur. In the south it is known at least as far as Pernambuco, and it probably grows still farther south. ARESCHOUG (1851 P. 14), for instance, says that it seems not to be rare on the coasts of Brazil (»ad oras Brasiliae non rara»). On the other hand, it is not known from the Atlantic coast of Africa, but from Durban (Port Natal) on the east coast (»In sinu Natalensi non infrequens» ARESCHOUG l. c.), and also from the Mascarene Islands (Mauritius) east of Madagascar. In her »Provisional List of the Marine Algae of the Cape of Good Hope» E. S. BARTON (MRS. GEPP) says that this plant »fide ARESCHOUG» has also been found at Table Bay (Capetown). This report seems, however, to be based upon some mistake, since ARESCHOUG reports it only from »sinu Natalensi» but says that it ought in the future to be sought for in Table Bay and at the Cape in general. ARESCHOUG says namely: »In sinu Tabulari et ad totam oram Capitis bonae spei, tum occi-

dentalem tum meridionalem prorsus desiderari videtur species, ad oras Brasiliae non rara» (Phyc. cap. P. 14). Thus it is not known from the southern or western coasts of South Africa.

This distribution is very remarkable in so far as the Alga has a very limited distribution in only the southwestern part of the Indian Ocean and does not at all occur in the Pacific. As *Chamaedoris* is hardly the kind of Alga that would be easily overlooked if it really occurred in an area, the absence of reports of its occurrence from the whole Indo-Malayan Archipelago can scarcely be due to any other reasons than that it really does not occur there. Surely it does not grow in Ceylon. Neither FERGUSON (cfr. MURRAY, 1887), HARVEY who have collected so many Algae there nor I myself have ever seen it.

The discontinuity in distribution of *Chamaedoris* is thus of a somewhat different kind than that of the other discontinuous tropical *Chlorophyceae*.

Cladocephalus (Fig. 10).

The genus *Cladocephalus* was established by HOWE in the year 1907 upon a species *Flabellaria luteofusca* first described by CROUAN. It has some resemblance in structure to *Aurainvillea* and *Udotea*. Three species are known (cfr. A. and E. S. GEPP, 1911 P. 59), of which *Cl. scoparius* HOWE is found at the Bahama Islands and *Cl. luteofuscus* (CROUAN) BÖRG. perhaps occurs at Guadeloupe and in the former Danish West Indies (St. Thomas), the third species, however, *Cl. excentricus* A. & E. S. GEPP occurs in the western part of the Indian Ocean, Mauritius (Fig. 10). *Cladocephalus* thus has no species common to the Atlantic and the Indian Oceans as *Chamaedoris* has; but it is remarkable that the Indian species has a marked western distribution. The genus is not found in the Pacific, and in this respect the resemblance in distribution to *Chamaedoris* is striking.

Owing to the remarkably western distribution in the Indian Ocean of these Algae and their absence from the Pacific it is tempting to suppose an earlier immigration via the Cape, which has now been broken off, just as MURRAY supposed. These Algae are — as far as I know — the only ones for which such explanations at first sight seem natural. But here we must consider that it is not, of course, entirely out of the question that they — or nearly related species — might be found in the Pacific. The possibility may also be taken into consideration that these Algae have died out in the interjacent zone.

In any case these Algae form in respect of geographical distribution a special group, the discontinuity of which — we may hope — will be explained in the future when a more detailed

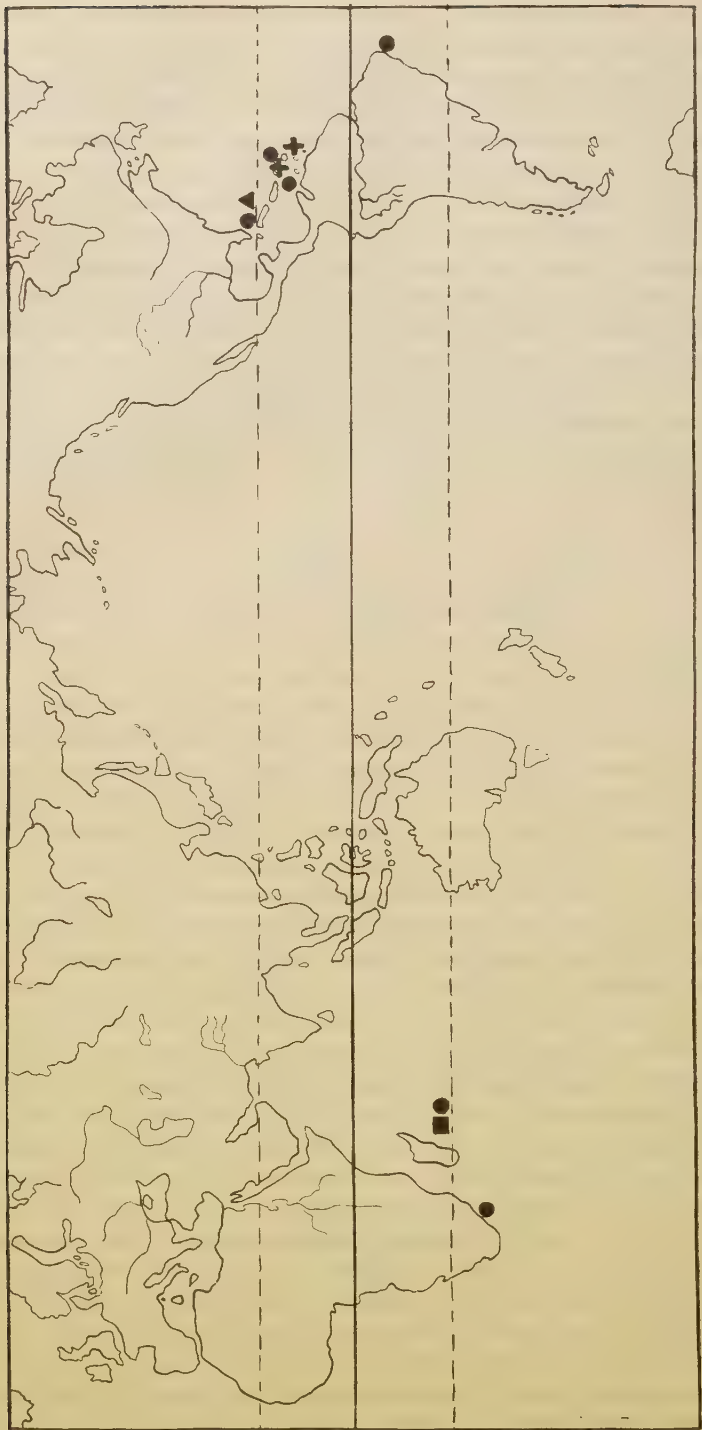

Fig. 10. The geographical distribution of *Chamaedoris* and *Cladocephalus*.

● *Cham. Peniculum.*, Atlantic, Indian.
■ *Cl. excentricus*, Indian.
▲ *Cl. scoparius*, Atlantic (West Indian).
+ *Cl. luteofuscus*, Atlantic (West Indian).

knowledge of their actual occurrence in the oceans has been obtained. At any rate their distribution does not influence the results which have been obtained regarding the causes of the discontinuous distribution of the other Algae treated above.

IV. Summary of results regarding the discontinuous distribution of the marine Algae which the Atlantic and the Indian-Pacific Ocean have in common.

A detailed critical investigation of the geographical distribution of the marine Algae which the Atlantic and the Indian Ocean have in common has thus strongly confirmed my theory concerning the importance of a former open connection between the Pacific and the Atlantic as an explanation of the present distribution of the marine plants. At its first publication in the year 1905 I based this theory exclusively upon the distribution of the marine Phanerogams and the Algal genus *Caulerpa*.

If now the importance for the distribution of the marine Algae of this open connection in Tertiary times between the two oceans may be assumed to be established, the question arises: has the Atlantic or the Indian-Pacific Ocean or perhaps both been the home of the species they have now in common? And if both have been centres for the origin of new species, which genera can be designated as Atlantic and which are Indian-Pacific?

Further it is evident that knowing the time when the connection was broken off, we can also to some extent determine at least the minimum age of a great number of Algae viz. of the common species which must have had this connection as the cause of their occurrence both in the Atlantic and the Indian-Pacific Ocean.

As to the first question it may be stated that there are genera the origin of which in all probability can be decided, but that there are also others which might have originated in either ocean with equal probability.

In most cases the Indian-Pacific Ocean seems more likely than the Atlantic to have been the centre of origin of new types.

Amongst the *Chlorophyceae* the following genera seem to belong to this category:

Halimeda (no specific Atlantic species known!).

Caulerpa (very few specific Atlantic species known!).

Amongst the *Phaeophyceae* especially:

Sargassum and *Dictyota*.

Amongst the *Rhodophyceae*:

Scinaia	The family *Squamariaceae*
Gloiophlaea	*Martensia.*
Galaxaura	

The following genera are evidently of Atlantic (or in some cases perhaps of Mediterranean) origin:

Dasycladus (Mediterranean)	*Penicillus*
Batophora	*Cladocephalus*

At present no genus is known of the *Phaeophyceae* nor of the *Rhodophyceae* which the two oceans have in common and which has the majority of its species in the Atlantic.

The following genera have about the same number of species in the two great oceans, making it impossible to decide anything about their supposed origin:

Chlorophyceae:	*Rhodophyceae:*
Valonia	*Liagora*
Neomeris	The family *Corallinaceae*
Aurainvillea	*Dictyurus.*
Udotea.	

From this list it is evident that of the genera rich in species and common to the two oceans only one viz. *Penicillus* is strikingly Atlantic. The other genera in common which are rich in species are either Indian-Pacific (the majority) or represented to about the same degree in the Atlantic and the Indian-Pacific Ocean. Apparently no safe conclusions regarding the origin of the latter group can be drawn at present.

Finally, as for the minimum age of the discontinuous tropical genera and species, it may of course be asserted, that since we know that the main connection between the two great oceans was broken during Miocene (VAUGHAN 1919, P. 611) or at the latest during Pliocene times viz. at the end of the Tertiary times, these genera and species must have been originated at or before that time. Thus they must be of at least Tertiary age.

Thus, all the genera and species in common which are discontinuous viz. do not occur at the southern points of Africa or America, must be said to have originated as early as late Tertiary times. To this category, then, the following genera must be reckoned:

Boodlea	with the species *B. siamensis.*
Microdictyon	» » » *M. umbilicatum.*
Anadyomene	» » » *A. stellata.*

Struvea with the species *Str. anastomosans.*
Valonia » » » *V. pachynema, utricularis,* and *ventricosa.*
Dictyosphaeria with the species *D. favulosa.*
Acetabularia
Neomeris with the species *N. annulata* and *dumetosa.*
Cymopolia
Aurainvillea
Rhipilia
Penicillus
Udotea with the species *U. flabellum.*
Halimeda with the species *H. Opuntia, gracilis,* and *incrassata.*
Caulerpa with the species *C. verticillata* J. AG., *crassifolia* (AG.) J. AG., *taxifolia* (VAHL) W. v. B., *sertularioides* (GMEL) HOWE, *Freycinetii* AG., *cupressoides* (VAHL) W. v. B., *clavifera* (TURN.) AG., *uvifera* TURN., *laetevirens* (MONT) J. AG., *Chemnitzia* (ESP.) LAMOUR., and *sedoides* (R. BR.) AG.

As to the *Phaeophyceae* there are certainly some species in common with discontinuous distribution but scarcely any genera, as they are regularly represented on the coast of South Africa by at least one or more species. These genera are, moreover, mostly critical, so that they are not yet suitable for comparisons, and no conclusions can be drawn from them regarding the age of the species.

The following genera of *Rhodophyceae* may, perhaps, owing to their distribution, be designated as originated before the break of the connection between the two oceans i. e. at the latest in late Tertiary times:

Liagora,
Dictyurus,
Martensia.

It is apparent that future investigations with new examples will in many respects further increase our knowledge of the remarkable discontinuity of the tropical marine Algae. It may perhaps be necessary in some way to alter the areas of distribution of some single species. The main lines thereof are, however, already so surely established that the theory of a former connection between the Atlantic and the Pacific Oceans being the real cause of the present geographical distribution of the tropical marine Algae may be deemed to have been proved. In this connection it may also be mentioned that the botanical authors who have lately had occasion to deal with these problems viz. BÖRGESEN and OSTENFELD have both fully adopted my theory.

It lies quite outside the plan of this work to consider the

further arguments for this theory which could be obtained from zoological investigations. It may, however, be mentioned that the first investigator to point out the striking likeness between the marine tropical fauna of the West Indies and that of the

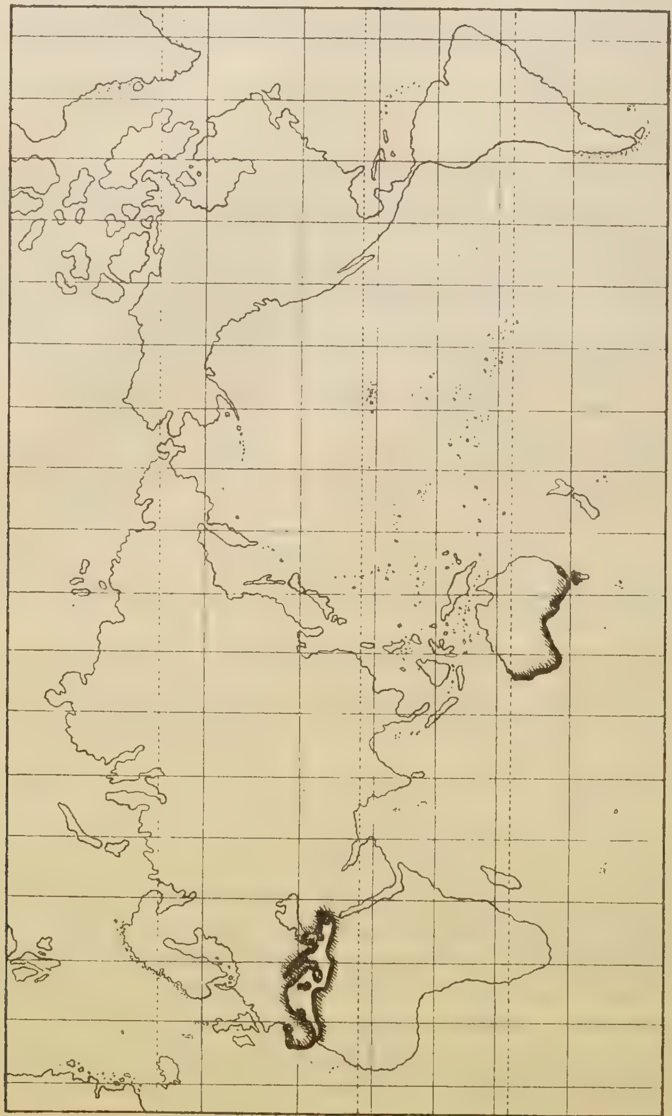

Fig. 11. The geographical distribution of the genus *Posidonia* ////// (From OSTENFELD). *P. oceanica*, Mediterranean (and at the Atlantic coasts of Spain and Portugal). *P. australis*, Indian (along the south and west coast of Australia).

Pacific and the reasons thereof seems to have been DUNCAN (1863), who undertook the study of the fossil corals of the West Indian Islands. Amongst other zoologists in later times who have dealt with the problem KÜKENTHAL (1916) may also be mentioned.

V. The discontinuous distribution of some marine Algae which are common to the Mediterranean and the Indian Ocean.

Many years ago, when ASCHERSON (1871) published his important paper »Die geographische Verbreitung der Seegräser», he called attention to the remarkable fact that the Mediterranean and the Indian Ocean (especially the Australian waters) had some marine Phanerogamic plants, sea-grasses, in common viz. the genera *Posidonia* and *Cymodocea*.

The genus *Posidonia* (of the family of *Potamogetonaceae*) has only two species, *P. oceanica* (L.) DELILE in the Mediterranean and the adjacent Atlantic coasts of Spain and Portugal, and *P. australis* J. D. HOOK. on the south-western and southern coast of Australia. Their distribution is moreover easily seen on the map (Fig. 11), which is reproduced from a paper by OSTENFELD (1918), who after ASCHERSON has devoted himself to the study of the sea-grasses more thoroughly than any other botanist.

The genus *Cymodocea* has some more species, about 8. One species, *C. nodosa* (UCRIA) ASCHERS., is common in the whole Mediterranean and the adjacent parts of the Atlantic coast of Africa (Fig. 12). Its nearest allied species, which together form a special subgenus *Phycagrostis* (WILLD.) ASCH., all belong to the Indian Ocean. Amongst these Indian species *C. rotundata* (EHRH. et HEMPR.) ASCHERS. et SCHWEINF., the most closely related species to *C. nodosa*, has a very wide range. The map (Fig. 12), also reproduced from OSTENFELD's paper, shows this distribution, from which it clearly follows, that *C. nodosa* and *C. rotundata* are typical vicarious species, one confined to the Mediterranean, the other to the tropical part of the Indian Ocean and adjacent parts of the western Pacific. The third species of this group *C. angustata* OSTENF. is hitherto only known from Western Australia (Fig. 12).

ASCHERSON concluded from this distribution that these two sea-grasses must have immigrated into the Mediterranean from the south-east. This must have taken place when the Mediterranean had an open connection with the Indian Ocean, which was the case in the Tertiary period. As a matter of fact, the sea-grasses are very old types. At least *Posidonia* is considered to have been found from Cretaceous times. A fact that even ASCHERSON had found striking if this hypothesis should prove to be right was that both *Posidonia* and *Cymodocea* are quite lacking in the Black Sea. But here OSTENFELD has supplied the explanation. In his paper on the sea-grasses from the »Danish Oceanographical

Expeditions 1908—1909 to the Mediterranean and adjacent seas» (1918) he has clearly shown that the hydrographical conditions in the Black Sea and the Sea of Marmora are quite different from those of the Mediterranean. The annual range of temperature

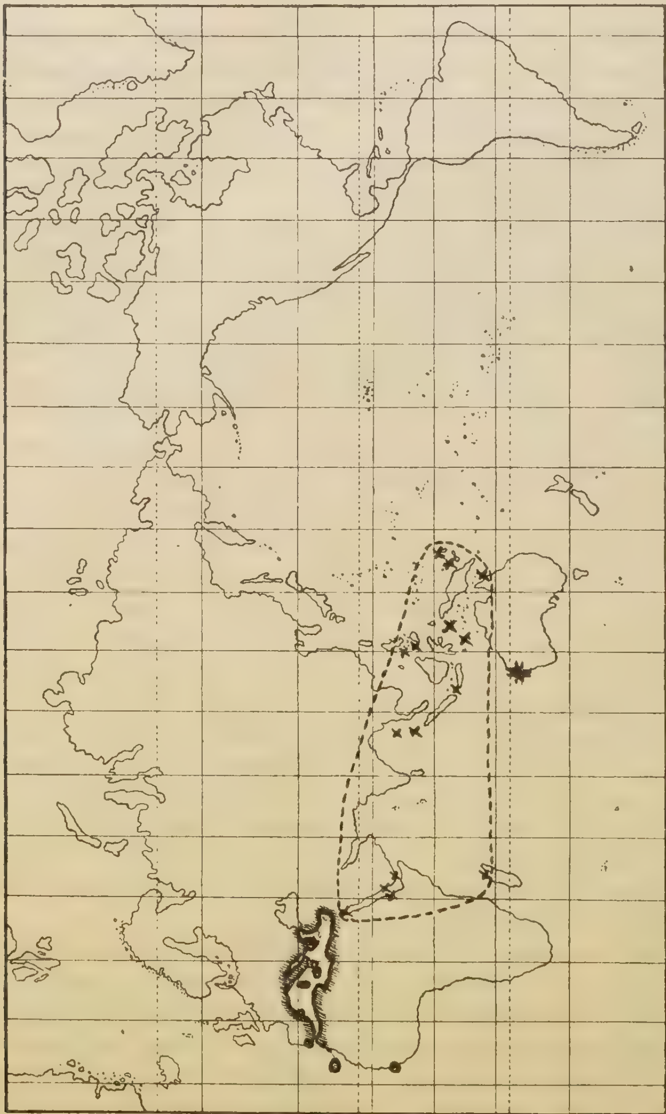

Fig. 12. The geographical distribution of the genus *Cymodocea*, subgenus *Phycagrostis* (From OSTENFELD). *C. nodosa*, Mediterranean (and at the adjacent Atlantic coast of Africa). × *C. rotundata*, Indian-Pacific (inclusively the Red Sea). ± *C. angustata*, Indian (only known from Western Australia).

is much greater in the Black Sea than in the Mediterranean. Particularly the winter temperature is much lower. Thus OSTENFELD (l. c. P. 12) after SCHOTT (1915) reports the Mediterranean surface temperature in the coldest season (February) to be

between 11° and 17° Celsius according to the locality, whereas the temperature of the Black Sea in the same season (February) is 6°—7° C, decreasing northwards to near 0° C. Now OSTENFELD has found that *Posidonia* and *Cymodocea* cannot generally thrive in places where the mean temperature falls below 10° C.

Moreover, the salinity of the Mediterranean is much higher (34—39 ‰) than that of the Marmora (21—22 ‰) and of the Black Sea (15—about 18 ‰). Thus there is an enormous divergence in the hydrographical conditions of the Mediterranean and the Black Sea, and this is — according to OSTENFELD — the proper explanation of the non-existence of *Posidonia* and *Cymodocea* in these seas. *Posidonia* and *Cymodocea* are subtropical, stenothermal, and stenohaline forms. It is not astonishing, then, that they do not occur at the present time in the Sea of Marmora and the Black Sea; and OSTENFELD's studies have afforded strong arguments in support of ASCHERSON's theory that the two specific Mediterranean sea-grasses, *Posidonia* and *Cymodocea*, must have immigrated into the Mediterranean from the south-east, during Tertiary times when there was open connection with the Indian Ocean.

That the Mediterranean has also received sea-grasses (for instance *Zostera marina*) from the west does not interest us so much in this connection.

The fact being now established that the Mediterranean must have received sea-grasses from the south-east i. e. from the Indian Ocean during Tertiary times, the question naturally arises: are there now in the Mediterranean any marine Algae which have immigrated from the south-east, from the Indian Ocean? This problem has — I believe — not previously been discussed. I think that even a preliminary investigation will show that this must be the case; and in the following I will try to give some examples hereof.

1. **Codiaceae.**

In the foregoing I have already partly dealt with the geographical distribution of the genus *Codium* from the point of view of the discontinuous distribution of the marine Algae. The recent monograph on the genus by SCHMIDT (1923) has rendered this quite an easy task, particularly as SCHMIDT has also, in a special chapter, discussed its geographical distribution. However, it seems to me that SCHMIDT has not been fully aware of some of the main principles for the proper understanding of the geographical distribution of the marine Algae. Therefore he has not been able to explain the remarkable distribution of certain species of the genus in question.

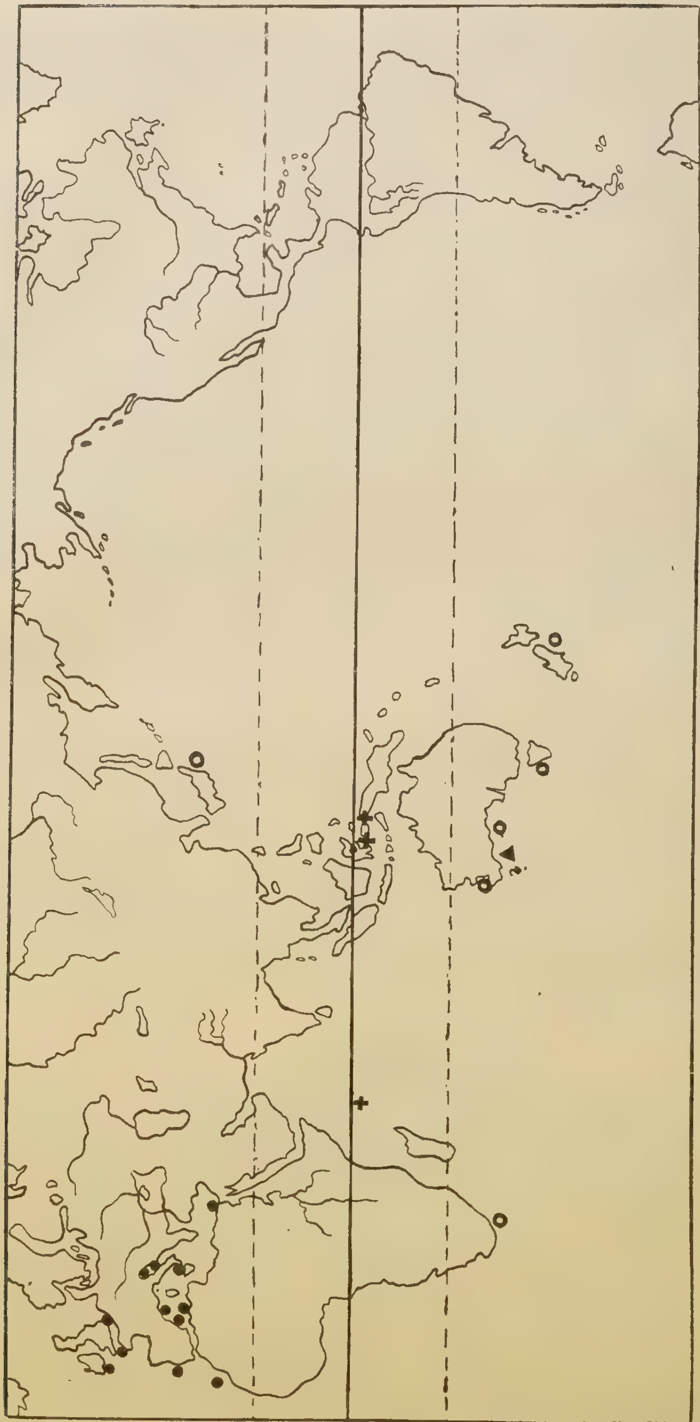

Fig. 13. The geographical distribution of the genus *Codium*, Sectio *Bursae*.

● *C. Bursa*, Mediterranean (and adjacent parts of the Atlantic).
+ *C. ovale*, Indian-Pacific (tropical).
○ *C. mamillosum*, Indian-Pacific (subtropical).
▲ *C. pomoides*, Indian (South-Australian?).

Thus regarding the geographical distribution of the section *Bursae* of *Codium*, SCHMIDT does not say anything except stating that its species — 4 in all — have two centres of distribution viz. one in the Mediterranean and another in the Indian-Pacific Ocean. However, it is easily seen (Fig. 13) that here we have a type of distribution which is quite analogous to that of *Posidonia* and *Cymodocea*.

The *Bursa*-group is very natural and well defined from the other species of the genus, characterized by the more or less spherical shape of their hollow thallus, which in its anatomical structure is distinguished by the club-shaped apices of the filaments (the »Blasen» of SCHMIDT) being unbranched, not forming dense clusters as in the group of *Adhaerentia*. The longest-known species *C. Bursa* (L.) C. AG., described already by LINNÉ, belongs to the Mediterranean flora. The map (Fig. 13) shows its distribution. It is spread over practically the whole of the Mediterranean and has also emigrated to the adjacent coasts of the Atlantic: in the south to the Canaries, in the north as far as to Ireland and the Channel (Belgian coast), but it does not occur in the West Indies. That is about the same distribution as *Posidonia oceanica* (compare Fig. 11), which, however, does not go so far north nor to the Canaries. Where, now, do we find the other members of the *Bursa*-group? The map (Fig. 11) gives us the information!

The nearest allied species to *C. Bursa* viz. *C. ovale* ZAN. is at home in the tropical Indian Ocean. It is found from the Seychelle Islands in the west through the Malayan Archipelago to the western part of New Guinea in the east. It is not met with outside the tropical zone.

The remaining species of the *Bursa*-group are also at home in the Indian Ocean. The species with the widest range is *C. mamillosum* HARV., which occurs at South Africa — the Cape — at Western and South Australia (Freemantle—Tasmania—New Zealand), thus giving an example of the many marine Algae which the Cape and South Australia have in common. But *C. mamillosum* seems also to occur on the Japanese coasts. The species thus has a very wide geographical distribution and occurs in the different localities in somewhat different forms (*α typicum* in Australia, *β capense* at the Cape, and *γ minus* in Japan). It is to be noticed that this species does not occur in the intermediate Malayan Archipelago. *C. mamillosum* is evidently not tropical but strikingly subtropical, just like *C. Bursa*.

It is curious that in the Indian-Pacific Ocean *C. mamillosum* shows an example of discontinuous distribution, and in these oceans *C. ovale* and *mamillosum* form a couple of so-called vicarious

species, the former apparently adapted to real tropical conditions (stenothermal?), the latter to more subtropical ones.

The fourth species of this group *C. pomoides* J. AG. is only known »ad oras Novae Hollandiae» without any further notice concerning localities.

When one knows this present distribution of the group, no great imagination is needed for the construction of the probable history of the evolution of the *Bursa*-group: It has once arisen somewhere in the Indian Ocean, whence one species, *C. Bursa*, has immigrated into the Mediterranean from the south-east. The others still remain in the Indian Ocean and have differentiated into 2—3 species: the tropical *C. ovale* and the subtropical *C. mamillosum* and *C. pomoides*.

The analogy with *Cymodocea*, subgenus *Phycagrostis*, is complete (compare Fig. 12). The only point of difference from *Posidonia* (Fig. 11) is that this genus is not represented by any species in the interjacent tropical part of the Indian Ocean.

Here it should also be borne in mind that the only Mediterranean *Halimeda*, viz. *H. Tuna* (ELL. et SOL.) LAMX., finds its nearest related species *H. cuneata* HER. in the Indian Ocean (comp. Fig. 9). There are practically only these two Halimedas which go outside the tropical zone. *H. cuneata* is found as far south as at the Cape (eastern side) and South Australia, but not in the Atlantic. Thus the two nearly related more subtropical Halimedas occur in the Mediterranean and the Indian Ocean. This fact seems to indicate that the Mediterranean *Halimeda Tuna* has immigrated into the Mediterranean from the south-east, although the distribution of the species might otherwise be just as well accounted for by an immigration from the Atlantic.

A third possibility is that *H. Tuna* has immigrated into the Atlantic from two directions, viz. to the West Indies from the Pacific via Panama, i. e. from the west, and into the Mediterranean from the Indian Ocean, i. e. from the south-east and thence to the Atlantic coast of Africa. We find, then, that the distribution of *Halimeda* is a rather complicated problem not easily solved.

What has now been said about *Halimeda Tuna* holds good also regarding *Penicillus mediterraneus*, already mentioned above (P. 28). This species has its most nearly related species in the Indo-Malayan Archipelago, although most of the species are chiefly at home in the West Indies. Under such circumstances an immigration into the Mediterranean from the south-east is not out of the question, but on the contrary rather probable.

That an immigration of these *Chlorophyceae* into the Mediterranean may have taken place from the south-east in the same

way as in the case of *Posidonia* and *Cymodocea* is the reason why the matter has been discussed in this chapter.

Dasycladaceae.

It seems to me that in the distribution of some members of the family *Dasycladaceae* we can also find examples of the same discontinuity as I have discussed just above. In a foregoing chapter (P. 25) I have dealt with this family viz. the group *Neomereae*. I will now point out some peculiarities in the distribution of the group *Dasycladeae*, comprehended as it was above on P. 21.

This group with its three genera: *Batophora*, *Dasycladus*, and *Chlorocladus* is very natural and may properly be divided into two subgroups:

a) *Batophora* with many lateral gametangia on each branch and

b) *Dasycladus* and *Chlorocladus* with only one seemingly terminal gametangium.

The geographical distribution of the group is shown on Fig. 14. *Batophora Oerstedii* J. AG. is confined to the West Indies including Bermuda. The Mediterranean *Dasycladus clavaeformis* (ROTH) C. AG. is also known from the Bermudas and the Bahama Islands, but curiously enough from no other parts of the West Indies. In the Mediterranean *Dasycladus* probably occurs in all parts although no trustworthy reports have yet been obtained from the eastern part. The eastern Mediterranean is indeed very imperfectly known. *Dasycladus*, just like *Codium Bursa*, also occurs in the adjacent Atlantic waters, e. g. at the Canaries and Madeira, but not on the Atlantic coast of Spain or Portugal.

Now the question arises: has *Dasycladus* entered the Mediterranean from the Atlantic or from any other direction? The fact that *Dasycladus* seems to be rather rare in the West Indies does not speak for its original home being there but for its having immigrated into this sea. On the other hand, the nearest allied genus to *Dasycladus* is *Chlorocladus*, of which the only known species *Chl. australasicus* SOND. (Cfr. SONDER, 1871) is found at Cape York in northern Australia (compare Fig. 14). This discovery is extraordinarily interesting because it shows that this characteristic group is also represented in the Indian-Pacific Ocean by a special genus. As this is most closely allied to the Mediterranean *Dasycladus*, it is not impossible that these two types have arisen in the Indian Ocean and that *Dasycladus* has immigrated into the Mediterranean from the south-east, i. e. the same way as *Posidonia*, *Cymodocea*, and *Codium Bursa*.

This supposition is, however, not certain. One may also

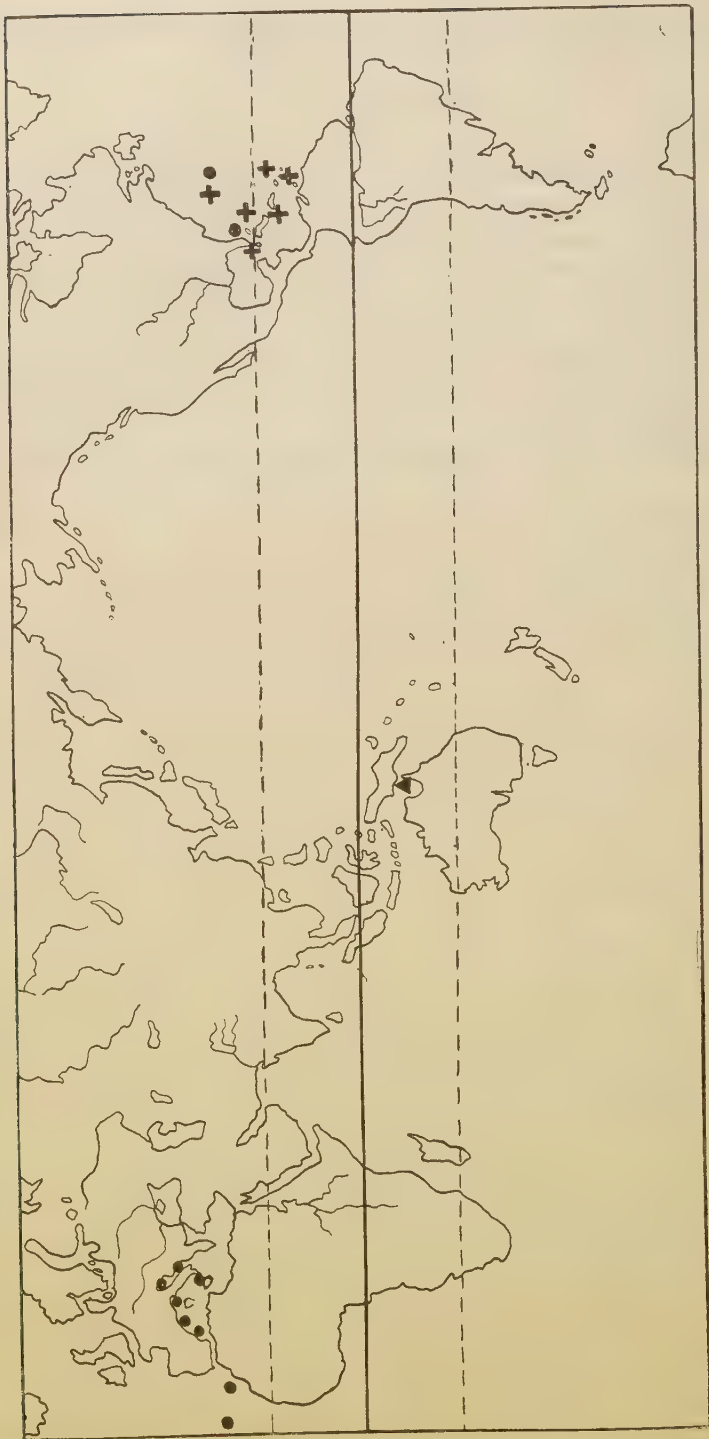

Fig. 14. The geographical distribution of the genera *Dasycladus*, *Chlorocladus* and *Batophora*.
● *D. clavaeformis*, Mediterranean, Atlantic. + *B. Oerstedii*, Atlantic (West Indian).
▲ *Chl. australasicus*, Indian-Pacific (N. Austr.).

suppose that the *Dasycladeae* arose somewhere in the Pacific and thence migrated westward into the Indian Ocean (Cape York) and eastward into the Atlantic via Panama and afterwards from the West Indies into the Mediterranean. Against this supposition is the fact that it is so rare in the West Indies and also that no representative of the group has been found in our time in the Pacific especially the South Sea islands. For the present the question may be left undecided. That an immigration from the south-east may be the most probable explanation of the occurrence of *Dasycladus* in the Mediterranean is, however, apparent. It is for this reason that I have treated this case of discontinuous distribution here.

Vidalia.

Finally I will mention an example of discontinuous distribution of this type obtained from a Red Alga. Though I do not yet know any Phaeophycean Algae with such a distribution, I believe that further investigations will perhaps show that the critical genus *Cystoseira*, so common in the Mediterranean, comprises some species whose path of migration has been south-easterly. Amongst the *Rhodophyceae* there is at least one genus which must have come from the south-east viz. the genus *Vidalia* of the family of *Rhodomelaceae*.

Vidalia volubilis (L.) J. Ag. is in the Mediterranean a rather common Alga, growing at comparatively great depths, and easily recognized by its curiously beautiful, spirally turned thallus. It is to be observed that this Alga also occurs in the Black Sea (Sebastopol), thus having a range from the Black Sea in the east to Cadiz, the Canaries, and the coast of Senegambia in the west. It is not known from any other parts of the Atlantic. As a curiosity it may be mentioned that it very often grows on old stems of *Posidonia oceanica*, which Alga, as we shall see, has the same distribution except for its occurrence in the Black Sea.

Where, then, is the home of the other species of *Vidalia*? Of about 8 species — *V. volubilis* excepted — which belong to this genus, only one occurs in the tropical Atlantic; all the others are indigenous in the Indian Ocean and the Pacific, especially on the coasts of Australia.

The Atlantic species *V. obtusiloba* (Mart.) J. Ag. is found on the Atlantic coast of South America from Vera Cruz in Mexico to Brazil. From the Antilles it is reported only from Martinique.

The remaining 7 species are all indigenous in the Indian Ocean and adjacent waters of the Pacific. Thus we find off south-western Australia:

V. spiralis Lamour., according to Harvey »very common» in western Australia;

V. gregaria FALKENB., at least from the Bay of Geraldton to Albany (King George Sound); and

V. intermedia J. AG. from Champion Bay, a species apparently nearly allied to *V. spiralis*.

From North Australia and New Caledonia we have *V. fimbriata* (R. BR.) J. AG.

From New Zealand we have *V. Colensoi* (HOOK. et HARV.) J. AG.

Thus no less than 5 species grow in Australian waters.

The remaining two species in the Indian Ocean have a more western distribution viz.:

V. Melvilli (J. AG.) SCHMITZ, which is found at Dar-es-Salam on the east coast of Africa, Madagascar, and Mauritius, and

V. serrata (SUHR) J. AG. from Port Natal (Durban) in South Africa.

No species is known from the South Sea Islands or generally speaking from the eastern Pacific Ocean.

If this distribution is studied, it is apparent that the centre of distribution of the genus lies in the southern Indian Ocean from Durban in the west to New Zealand in the east, where the majority, 7 species, belong. Further, there is one species in the Black Sea and the Mediterranean and one in the western Atlantic. The genus cannot be characterized as tropical since only two species (*V. fimbriata* and *V. Melvilli*) are found inside the tropical zone. It may rather be characterized as subtropical. The analogy of distribution to *Posidonia* and *Cymodocea* is striking. Especially the fact that *V. volubilis* also occurs in the Black Sea is very interesting (comp. P. 51). Without any doubt it can be affirmed that *Vidalia volubilis* has immigrated into the Mediterranean from the south-east from a former common centre in the Indian Ocean, whence the other species have migrated to the southern parts of the Indian Ocean. In the tropical zone proper the genus has for the most part died out just like *Posidonia*. This explains the discontinuous distribution at the present time! Under such conditions it is probable that the West Indian species, which also occurs on the coast of Brazil, has arrived there from the east, perhaps from the Mediterranean. In any case it seems not to have come across Panama.

Scinaia.

Also *Scinaia furcellata* may perhaps be reckoned to the same group as *Vidalia volubilis* regarding its geographical distribution, its most nearly related species being at home in the Pacific, not in the Atlantic (Cfr. P. 36). This is, however, less certain, as the Indian species are not the nearest related to *Sc. furcellata*.

Thus the path of migration into the Mediterranean for this species must be designated as very uncertain.

In the foregoing I have shown that the peculiar and at first sight very inexplicable distribution of *Posidonia* has its evident analogies in the distribution of some marine Algae of several classes, *Chlorophyceae* and *Rhodophyceae*, which have apparently come into the Mediterranean from the south-east in Tertiary times when that sea had open connections with the Indian Ocean.

VI. **Summary.**

In the foregoing I have in detail demonstrated that the present discontinuous distribution of many marine Algae can be comprehended only when we take into consideration the great changes in the relations between land and sea which have taken place since Tertiary times.

There are two oceans especially the present marine vegetations of which show clearly that they must have arrived by ways which nowadays are broken by continents viz.:

the American tropical Atlantic (the Caribbean Sea), which has received a good deal of its marine plants (Phanerogams and marine Algae) from the west when the open connection with the Pacific still existed, and

the Mediterranean, which has received besides some Phanerogams several marine Algae from the south-east when the open connection with the Indian Ocean still existed.

It would in this connection have been interesting from several points of view to discuss, with special regard to the geographical distribution of the marine Algae, WEGENER's well-known hypothesis of the wandering or drifting apart of the present Continents from an original continuous land mass; but for this our algological knowledge may be considered too scanty. It will be noticed, however, that my researches show that the majority of the older genera of Algae have evidently had their main distribution in the Indian-Pacific Ocean, whence they have migrated into the Atlantic. Only in one or two cases does the migration seem to have gone in the opposite direction. Thus, the Alga-flora of the Atlantic may perhaps be considered younger than that of the Indian-Pacific Ocean. This does not contradict WEGENER's theory, according to which the Atlantic is of much younger date than the Indian-Pacific Ocean.

In any case we find that the great changes which have taken place on the earth since Tertiary times and which have caused such great changes in the relation between land and sea can to this very day be traced in the present geographical distribution of the marine Algae.

Finally I seize the opportunity to thank Professor C. H. OSTENFELD of the Botanical Museum, Copenhagen, for his kind permission to copy in this paper some of the maps (Fig. 1, 2, 11, 12) from his publications on the geographical distribution of the sea-grasses.

Upsala, Botanical Institute, Nov. 1923.

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Contents.

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ARKIV FÖR BOTANIK.
BAND 19. N:o 4.

The Lower Liassic Flora of Sofiero and Dompäng in Scania.

By

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Communicated Nov. 28th 1923 by C. A. M. LINDMAN and A. O. GAVELIN.

Introduction.

Among the large material of Mesozoic plants from Scania in the Palaeobotanical Department of the State Museum of Natural History at Stockholm there are two small collections, from Sofiero and Dompäng, respectively, which have not yet been described.

During the time of my studies at the palaeobotanical department, Professor T. G. HALLE suggested to me that I should describe the material from these two localities.

The material from Sofiero described in this paper was collected in 1875 by the late Professor A. G. NATHORST. The collection from Dompäng was chiefly brought together in 1906 by Mr. V. LINDKVIST. A few specimens presented by H. R. H. THE CROWN PRINCE and by Prof. A. G. NATHORST have been added later.

The fossil plants from Sofiero are chiefly preserved in a very fine-grained thin-bedded sandstone. The cuticle is often preserved as a carbonaceous film. The fossils from Dompäng are only impressions in a ferruginous sandstone. Both localities belong to the Lower Liassic.

To the director of the palaeobotanical department, Prof. T. G. HALLE, I desire to render my sincere thanks for much helpful instruction in connection with this paper.

Description of the Species.

Equisetites Mobergii Möller.

See Halle 1908, p. 26; pl. 4, figs. 38, 39. The species is found at Dompäng.

Equisetites sp.

Pl. 1, fig. 1.

In pl. 1, fig. 1, is shown a fragment of an *Equisetites*-stem from Sofiero. The specimen, which represents two internodes of the stem and traces of two nodes, measures about 7 to 10 mm. in breadth; the internode is 35 mm. long. One node shows only traces of three commissural furrows. At the other node there are four similar furrows, about 5 mm. long.

The specimen resembles *Equisetites praelongus* Halle[1], but the internodes are much shorter. It is, however, too badly preserved to be definitely determined.

Cf. **Thaumatopteris Schenki** Nath.

Pl. 1, fig. 6.

Thaumatopteris Schenki, Nathorst 1907, p. 3; pl. 1, figs. 1—11; pl. 2.
» » Antevs 1919, p. 13; pl. 1, fig. 4.
For further references see Antevs, l. c.

Fig. 6, pl. 1, represents a fragment of a fern-pinna from Dompäng. The pinnules are attached to the rachis with the whole of their bases and at almost right angles. They are narrow and wedge-shaped, bending slightly forward. The margin of the pinnules is entire. The midrib is distinct throughout the whole lamina, while the lateral veins are badly preserved; with the aid of a hand-lens, however, they can be observed to form anastomoses. The fragment probably belongs to a young leaf.

Th. Schenki Nath. has been found at many other localities in Scania besides Dompäng, and is also known from Franconia, Poland and Bornholm.

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[1] Halle 1908, p. 16; pl. 3, figs. 19—26; pl. 4, figs. 1—16.

Dictyophyllum Nilssoni (Brgn.) Göpp.

Pl. 2, fig. 1.

Dictyophyllum Nilssoni, Nathorst 1906, p. 5; pls. 2, 3.
For further references see Nathorst, l. c.

The species occurs both at Dompäng and Sofiero. At Dompäng it is represented by a fragment preserved in a fine-grained sandstone, shown in pl. 2, fig. 1. The apex and base of the segment are wanting, but the venation is distinct, anastomosing to form the characteristic meshes. The rachis of the segment is very broad, measuring 4 mm. across, and is deeply impressed into the matrix. The midribs of the lateral lobes arise at an angle of about 60°, and are about 1 mm. broad; the secondary and tertiary veins form a network, which is fairly open, the meshes being hexagonal or rhombic.

Another fragment of the species, not figured here, has been found at Sofiero. It consists of a part of a segment with several lobes which form an angle of about 60° to the rachis. It is very much like the specimen from Dompäng just described.

In regard to the characteristic venation and the size of the segments, the specimens from both localities agree very well with *Dictyophyllum Nilssoni* (Brgn.), Göpp., var *genuinum* Nath. (Nathorst 1906; pl. 3, figs. 4—5).

Besides occurring at Sofiero and Dompäng, *D. Nilssoni* occurs commonly at Pålsjö, Hälsingborg and Hoer in Scania, and has also been found in Bornholm, Poland, Franconia, and in China. It is rather more characteristic of the Liassic than of the Rhaetic.

Cf. **Andriania baruthina** F. Braun.

Pl. 1, figs. 2—5.

Andriania baruthina, Gothan 1914, p. 102; pl. 17, fig. 8; pl. 18, figs. 1—2.
» » Antevs 1919, p. 17; pl. 1, figs. 10—15.
For further references see Gothan, l. c.

The only two fragments of the fossil from Sofiero are the counterparts of each other, representing the impressions of both sides of the pinnules. The pinnules are regularly divided up into more or less square fields, corresponding each to the area between two adjacent tertiary veins, which arise at about right angles from the secondary veins of the pinna (pl. 1, figs. 3, 5). The lateral veins on the impression of the

lower side of the lamina appear as furrows, while those on the counterpart are elevated. The secondary veins of the pinnae are giwen off at very wide angles, but they bend slightly towards the distal end of the pinna. The specimen is so badly preserved that besides the midrib, the secondary veins and the characteristic square fields of the pinnules, no further details can be observed.

In view of the characteristic form of the fields separated by the secondary veins of the pinnules, and the close disposition of the pinnules, the specimen is probably identical with *Andriania baruthina* F. BRAUN. It is, however, very difficult to distinguish this genus from *Gutbiera.*

Besides from Sofiero, *Andriania baruthina* is already known from the Lower Liassic beds of Hoer in Scania, from the Rhaetic of Billesholm, from Franconia and from Hungary (GOTHAN, l. c., p. 13).

Sagenopteris Nilssoniana (BRGN.) WARD.

Pl. 1, figs. 7—10.

Sagenopteris Nilssoniana, HALLE 1910, p. 6; pl. 1, fig. 24; pl. 2, figs. 15—23; pl. 3, figs. 6—11.
» » ANTEVS 1919, p. 21.
For further references see HALLE, l. c.

The largest, yet incomplete, pinna of this species from Sofiero, not figured, measures about 11 cm. in length and 3,5 cm. in breadth, and is of a broadly lanceolate form. The surface of the impression is covered with a carbonaceous film, in which the structure of the cuticle is usually preserved. The pinna has a distinct midrib from which the secondary veins are given off at acute angles; the veins anastomose to form narrow meshes.

There is another specimen, not figured, from Sofiero, showing four pinnae attached to a petiole reaching a length of 65 mm. with a breadth of 3,5 mm. Such a long petiole is not often found in the Swedish material of the species.

The specimen shown in fig. 10, pl. 1, probably represents a young individual of this species. It consists of three oval pinnae, each measuring 15 mm. in length and 8 mm. in breadth. Though the petiole is absent, there is hardly any doubt, from the relative position of the pinnae, that these belong to the same leaf. The midrib and the lateral veins are very indistinct; but this is due solely to the condition of preservation. The development of the midrib is subject to great variation

in this genus, and is not of much value as a distinction of species.

In addition to the specimens now described, which are all from the so-called »Slipsandstenen» of Sofiero, there is one single pinna in a dark bluish-grey shale probably belonging to the next higher bed with *Cyclas Nathorsti.* It is a lanceolate pinna, which measures 33 mm. in length and 11 mm. in breadth. The venation and the general shape of the pinna are very characteristic of the species; the small size seems to indicate that the specimen represents a pinna of a young leaf.

In the micaceous sandstone of Dompäng some incomplete pinnae are also found. The specimen shown in pl. 1, fig. 9, is the largest and most complete pinna from this locality; it is of a lanceolate form, and measures 70 mm. in length and 21 mm. in breadth in the middle of the pinna. The apex of the lamina tapers rather suddenly towards the distal end. The specimen represents the impression of the lower surface of the pinna. The midrib appears as a furrow in the lower part of the pinna; in the upper part it is absent. The lateral veins are, as usual, given off from the midrib at acute angles, and anastomose to form narrow meshes.

The specimen shown in fig. 8, pl. 1, represents the impression of the upper surface of a fragmentary pinna; the midrib and the lateral veins and their meshes are very distinct.

Besides occurring at Sofiero and Dompäng, *S. Nilssoniana* has been found at Pålsjö and Hoer and possibly also at Rödalsberg in South-eastern Scania. Pålsjö and Rödalsberg belong to the Uppermost Rhaetic, Hoer to the Lower Liassic.

Marattiopsis hoerensis (Schimp.) Thomas.

Pl. 2, figs. 2—3.

Marattiopsis hoerensis, Antevs 1919, p. 21; pl. 2, figs. 2—13; pl. 6, fig. 40. For further references see Antevs, l. c.

The specimens from Sofiero are preserved in a fine-grained thin-bedded sandstone. They are only fragments of the linear pinnae, the apices of which are usually wanting. The largest, yet incomplete, specimen measures 17 cm. in length and 3,6 cm. in breadth. If the pinna has the same relation between length and breadth as the longest one from Hoer, which is 30 cm. long and only 2,5 cm. broad (Antevs l. c.; pl. 2, fig. 6), the entire length ought to have been considerably more than twice that of the preserved portion.

The specimens are unfavourably preserved; the indistinct linear synangia above the secondary veins and the stout midrib of the pinna are shown, but the details of the venation are indistinct. The secondary veins seem to be fine, and to be closely placed. The bifurcation of the secondary veins takes place midway between the midrib and the margin. In all the specimens from Sofiero linear synangia are shown placed above the lateral veins; they extend for about one half of the distance from the margin to the midrib. The fine striation on the midrib, as observed in *Marattiopsis anglica* THOMAS (1913, p. 228) from the Cleveland district of Yorkshire, is not seen in these specimens.

In fig. 3, pl. 2, the characteristic oblique-cordate base of the pinna is very clearly shown. In view of the large size of the pinna, the characteristic base and the venation, the specimens must be regarded as specifically identical with *Marattiopsis hoerensis* (SCHIMP.) THOMAS from the Hoer sandstone.

Besides from Sofiero, *Marattiopsis hoerensis* is only known from the Lower Liassic of Hoer.

Nilssonia polymorpha SCHENK.

Pl. 2, figs. 4—6.

Nilssonia polymorpha, NATHORST 1909, p. 10; pl. 5, figs. 9—13; pl. 6, figs. 9—13; pl. 7, fig. 20; pl. 8, figs. 12—18.
» » ANTEVS 1919, p. 26.
For further references see NATHORST, l. c.

The specimens of this species from Dompäng (figs. 5, 6) consist partly of isolated truncate segments, partly of fragments of undissected leaves with remains of the lamina preserved on both sides of the rachis. The lamina of the dissected leaves is broader than that of the undivided ones, which are probably young leaves. The lateral veins are parallel and are given off almost perpendicularly from the rachis. In the narrow leaves the venation is very dense; in the broader ones the distance between the lateral veins is greater, or about 1 mm. Fig. 6, pl. 2, represents an impression of the upper surface of the leaf, the middle furrow being represented by an elevated ridge.

The specimens from Sofiero are only three in number. One of these, shown in fig. 4, pl. 2, represents the lower side of a long and narrow leaf. The lower part of the specimen is entire, the upper part is partly dissected, at least in the left half. The other two specimens from Sofiero are fairly well

preserved as impressions with a coating of black carbonaceous matter. The leaf is dissected into truncate segments of unequal breadth. The dissection either reaches the rachis or only midway between the rachis and the margin. The broadest leaf measures 22 mm. in breadth and was considerably more than 90 mm. long. Both specimens represent impressions of the lower side of the leaf, the midrib appearing as a furrow in the matrix.

Besides occurring at Sofiero and Dompäng, *Nilssonia polymorpha* has been found in many other localities both in Scania and in other parts of the world.

Anomozamites gracilis NATH.

Pl. 1, figs. 11—12; pl. 2, fig. 12.

Anomozamites gracilis, NATHORST 1876, p. 43; pl. 12, figs. 4—12.
» » HALLE 1915, p. 517; pl. 13, figs. 16, 17, 21.
» » ANTEVS 1919, p. 34; pl. 4, figs. 27—29.
For further references see ANTEVS, l. c.

This species is represented at Sofiero by only four fragments preserved as impressions with a carbonaceous film in a grey fine-grained sandstone. The cuticle seems to have been leathery and resistant, and, in favourable cases, can be detached from the rock. The lamina of the leaf is more or less regularly dissected into rectangular or rhombic segments, which are attached to the sides of the rachis. The rachis of one of the fragments is so distinct that the bilateral attachment of the segments is very clearly shown.

The largest specimen from Sofiero measures about 90 mm. in length and 15 mm. in breadth (fig. 12, pl. 2). It is divided into truncate segments alternating on both sides of the rachis. The segments are rather short and broad, especially towards the petiole of the leaf.

If the carbonaceous film is treated with nitric acid and chlorate of potash and afterwards transferred to ammonia, it shows the outlines of the epidermal cells. The cuticle is not well preserved in this case, however, and the walls of the epidermal cells are only indistinctly shown. The epidermal cells of the better preserved part of the cuticle are seen to be isodiametrical, and to have somewhat sinuous walls. The margin of the segment is not thickened as in the case of *Anomozamites marginatus* (UNGER) NATH. from Pålsjö and Bjuf in Scania. The stomata are irregularly scattered over the whole surface; and the structure of the epidermis does not

indicate the course of the veins. In this respect the epidermis is more like that of *Anomozamites marginatus* (HALLE l. c., p. 518). The epidermis, however, is too badly preserved to be of much value for the determination. Morphologically the characters of the leaves show a close agreement with *Anomozamites gracilis* NATH.

Besides occurring at Sofiero, this species has also been found at Pålsjö, Bjuf, Höganäs and Hoer, and in Franconia.

Ginkgo Hermelini (NATH.) HARTZ.

Pl. 1, figs. 13—15.

Gingko (Baiera?) Hermelini, HARTZ 1896, p. 240; pl. 19, fig. 1.
» » NATHORST 1906 a, p. 15.

This species was first found at Sofiero in Scania and then at Cape Stewart in Greenland. As already mentioned by HARTZ (l. c.), the specimens from both Greenlend and Scania are imperfectly preserved though the venation of the Scanian specimen is more clearly shown. It is also stated that, owing to the absence of the base in the specimens from both localities, it is impossible to decide whether the leaves should be referred to *Ginkgo* or to *Baiera.*

Fig. 13, pl. 1, shows the specimen from Sofiero; the leaf is broadly fan-shaped, deeply dissected into 6 more or less equal segments. It shows the sharp delimitation of the leaf towards the petiole. HARTZ stated that the base is absent in the Scanian specimen, as in the one from Greenland. The same specimen, as figured here, shows the base very clearly, but this is due to subsequent preparation undertaken in connection with this description. The segments are oblanceolate to oblong, their length varying from 45 to 55 mm., their breadth from 7 to 10 mm. The veins are about 7 in each segment, a comparatively small number in proportion to the breadth.

Figs. 14 and 15 show two specimens from Dompäng. The lobes of the leaves are somewhat smaller and narrower than those of the specimen from Sofiero. The veins are distinct, 6—8 in each lobe. In the general characters these two specimens agree very well with the specimen from Sofiero.

In shape and size all the Scanian specimens closely resemble HARTZ' specimen of *Ginkgo Hermelini* from Cape Stewart.

Since it has become possible to examine the base of the leaf from Sofiero, there can no longer be any doubt, in regard

to the sharp delimitation of the lamina towards the petiole, that the species should be referred to *Ginkgo*.

Except at Sofiero and Dompäng, this species has only been found at Cape Stewart in eastern Greenland.

Ginkgo or Baiera sp.

Pl. 1, fig. 20; pl. 2, fig. 7.

The specimens shown in fig. 20, pl. 1 and in fig. 7, pl. 2, as well as another similar fragment, all from Sofiero, cannot with certainty be determined specifically or even generically. There is a certain general resemblance to *Ginkgo Geinitzi* NATH. (NATHORST 1876, p. 68, pl. 13, fig. 17 [as *Baiera taeniata* BRAUN?]. ANTEVS 1919, p. 43; pl. 5, fig. 18), provided that the segments in NATHORST's type-specimen from Pålsjö are broken and do not show the upper part.

Baiera taeniata F. BRAUN.

Pl. 1, figs. 16—18.

Baiera taeniata, F. BRAUN 1843, p. 21.
» » SCHENK 1867, p. 26; pl. 5, figs. 2 [(?)1, 3, 4]; pl. 6, figs. 1—2.
» cf. » NATHORST 1906 a, p. 15.
» cf. » » 1910, p. 508.
» » GOTHAN 1914, p. 150; pl. 29, fig. 2; pl. 31/32, fig. 1.
» » ANTEVS 1919, p. 44; pl. 5, figs. 20—24; pl. 6, fig. 43.
» » JOHANSSON 1922, p. 46; pl. 4, figs. 7—8; pl. 8, fig. 12.

The segmentation of the leaf in this species is characteristic. The first bifurcation, dividing the leaf into two equal halves, extends down to the top of the petiole, while the secondary and tertiary bifurcations do not reach so far down. The outer segments formed by the secondary bifurcation usually bifurcate once more than the inner ones, i. e. the tertiary bifurcation of the inner lobes does not always take place. The number of segments in a leaf thus varies from 4 to 8. The leaf is sometimes asymmetrical, one side being more developed than the other.

Fig. 16, pl. 1, represents a specimen from Sofiero with only four segments; the distal part of the outer and the basal portion of the inner segment to the left are wanting, so that the specimen seems to have only three segments. The longest segment measures about 90 mm. in length and 8 mm. in breadth. The form of the segments is linear or linear-lanceo-

late; their apices are obtuse. The veins are few and very conspicuous, parallel to the margin of the lobes.

Fig. 18, pl. 1, is another example of this species from Sofiero; the segments of this leaf are a little shorter and more asymmetrical than those of fig. 16.

Fig. 17, pl. 1, is a specimen from the Dompäng sandstone, consisting of four large segments, the distal portions of which are wanting. These four segments are so arranged that three of them belong to the right half of the leaf, while only one segment is preserved on the left. The petiole is about 30 mm. long. The veins of the segments are strong and bifurcating. The largest segment measures 8 mm. in breadth and 60 mm. in length without being complete. In general habit this specimen is very similar to one of the specimens from Hoer (ANTEVS l. c.; pl. 5, fig. 22).

The fossil from Dompäng is preserved in sandstone, and shows no cuticle attached to the impression. The cuticle of the leaves from Sofiero is preserved as a carbonaceous film, which can be detached from the matrix. This film, after treatment with nitric acid and chlorate of potash, and subsequent transferring to ammonia, can be examined under the microscope.

The outlines of the epidermal cells are rather well preserved. The stomata occur on both sides of the segments, but there is some difference in their distribution. On one side they form broader bands, each of which consists of about 5—7 single rows of stomata. The stomatiferous bands are separated from each other by narrow non-stomatiferous zones of elongated cells in seriate arrangement. These non-stomatiferous zones evidently mark the course of the veins, as in other similar cases. The stomata on the other side of the segment occupy almost the whole surface, and form single rows without regular non-stomatiferous bands of tissue between them. No papillae can be observed in the specimens from Sofiero, while in the leaves from Hoer and Stabbarp they are well preserved. In both cases, however, the outlines of the epidermal cells and the stomata are very similar.

Besides occurring at Sofiero and Dompäng, *Baiera taeniata* has been found at Hoer and Stabbarp, and also in Franconia and Austria.

Baiera cf. angustiloba HEER.

Pl. 1, fig. 21.

Baiera angustiloba, HEER 1878, p. 24; pl. 7, figs. 2, 2 b.
» » » 1880, p. 14; pl. 3, figs. 1—3.
» cf. » ANTEVS 1919, p. 46; pl. 5, fig. 26.
» » » JOHANSSON 1922, p. 48; pl. 1, fig. 27 (28); pl. 8, figs. 10—11.

In pl. 1, fig. 21, are shown fragments of one or more leaves of a *Baiera*, which is closely comparable to *Baiera angustiloba* HEER from Siberia, though its lobes are a little narrower. The leaves of this species, through repeated bifurcation, are dissected into several narrow lobes, which measure about 1,5—2 mm. in breadth. Each lobe has only 3—4 veins.

The fossil from Sofiero consists of an impression in a grey fine-grained sandstone covered with a carbonaceous film, which can be detached from the matrix and examined microscopically after the usual treatment: the cuticle, however, is very badly preserved. The stomata are sparse; they form several uniseriate rows, which are separated from each other by non-stomatiferous bands of longitudinally arranged rectangular cells.

The arrangement of the stomata of this specimen is a little different from that of *B. cf. angustiloba* from Stabbarp. In the latter species the stomata are more densely placed, in broader, non-seriate bands separated from each other by broad non-stomatiferous zones of rectangular cells (JOHANSSON l. c., p. 48; pl. 8, figs. 10, 11).

Unfortunately the cuticular structure of the type-specimen from Siberia is unknown, so there is no possibility of comparing the microscopical characters.

In view of the morphological similarity of this specimen to those from Hoer, Stabbarp and Siberia, I venture to place it under the name *Baiera cf. angustiloba.*

Besides from Sofiero, the species is only known from the localities mentioned above.

Baiera cf. spectabilis NATH.

Pl. 1, fig. 19.

For references see JOHANSSON 1922, p. 45.

In pl. 1, fig. 19, is represented a small fragment of a *Baiera*, which is too imperfect to be definitely determined, but seems to be well comparable with *Baiera spectabilis* NATH. from Stabbarp.

The specimen from Sofiero represents the upper part of a bifurcating segment. The ultimate segments thus formed measure about 3 mm. in breadth and 25 mm. in length without being complete. Their bases are 7 mm. broad (compare NATHORST, 1906 a; pl. 1, fig. 8; pl. 2, fig. 1).

The veins are distinct; the distance between each two veins is 1 mm., their bifurcation is not well shown. The

shape and the size of the lobes so strongly recall *Baiera spectabilis* NATH., that there cannot be much doubt about the identity, in spite of the fragmentary nature of the specimen.

Baiera spectabilis NATH., which is one of the most large-leaved species of the genus, has hitherto been found, besides at Sofiero, at Stabbarp and Hoer.

Baiera cf. Czekanowskiana HEER.

Pl. 2, fig. 8.

Baiera Czekanowskiana, HEER 1876, p. 56; pl. 7, fig. 1; pl. 10, figs. 1—5.
» » » 1880, p. 12; pl. 1, fig. 12; pl. 2, figs. 1—3; pl. 3, figs. 4—8.
» » MÖLLER 1903, p. 27; pl. 5, fig. 3.

The fossil from Sofiero represents parts of four linear segments of a dichotomously divided leaf. The longest segment preserved measures 65 mm. in length and 3 mm. in breadth. The petiole of the leaf, or the common base of the four segments, is 30 mm. long and 2 mm. broad. If compared with the inconsiderable breadth of the segments, this basal part or petiole is thus very broad. The length of the preserved part of the leaf is about 10 cm. The venation is very badly preserved.

The single specimen represented in the collection is from Sofiero. It is closely comparable with the Siberian specimens of *Baiera Czekanowskiana* HEER. Some of the Siberian specimens figured by HEER under different specific names, as *Baiera angustiloba* and *Baiera Czekanowskiana*, are rather like each other in regard to the bifurcation and the size and shape of the segments; all these specimens may therefore belong to one and the same species (compare HEER 1880; pl. 3, figs. 1—7). To settle this question, however, it would be desirable to examine the type-specimens, and I have therefore kept HEER's names.

Besides occurring at Sofiero, *Baiera Czekanowskiana* has hitherto been found only in Siberia and in Bornholm.

Czekanowskia rigida HEER.

Pl. 2, fig. 9.

Czekanowskia rigida, HEER 1876, p. 70; pl. 5, figs. 8—11; pl. 6. fig. 7; pl. 10, fig. 2 b.
» » NATHORST 1886, p. 96; pl. 20, fig. 6.
» » » 1906 a, p. 11; pl. 1, fig. 9; pl. 2, figs. 2—15.
» » ANTEVS 1919, p. 47; pl. 5, figs. 28—29.
» » JOHANSSON, 1922, p. 49; pl. 8, fig. 6; textfig. 5.
For further references see NATHORST 1906 a, p. 11.

This species is represented at Sofiero by several fragments, which are all very badly preserved. The best specimen, as shown in pl. 2, fig. 9, consists of three segments, probably belonging to one and the same short shoot, perhaps to the same leaf. They are very similar to some specimens from Stabbarp and Hoer in Scania.

Czekanowskia rigida is a very widely distributed species; besides from Sofiero, it has been recorded from Bjuf, Stabbarp, and Hoer in Scania and also from Bornholm, Poland, Greenland, Siberia and China.

Palissya sp.

See NATHORST 1908, p. 9; pl. 1, figs. 19—22. The specimens are from Sofiero.

Pityophyllum longifolium (NATH.) MÖLLER.

Pl. 2, figs. 10—11.

Folium (arboris?) lanceolato-lineare, E. FRIES in: NILSSON 1820, p 285; pl. 5, fig. 7.
Cycadites? longifolius, NATHORST 1876 (1878 a), p. 47 (25); pl. 13, figs. 1—3.
Pityophyllum longifolium, MÖLLER 1903, p. 40; pl. 6, figs. 9—11.
» » ANTEVS 1919, p. 49; pl. 6, figs. 1—2.
For further references see ANTEVS l. c.

In the collection from Dompäng there are several fragments of linear leaves of the *Pityophyllum*-type. Two of these specimens are figured in pl. 2, figs. 10, 11. The longest specimen, without being complete, measures about 100 mm. in length and 5 mm. in breadth. It narrows gradually towards the apex and base. In both specimens figured the impressions clearly show a marked longitudinal furrow caused by the thick midrib; the fine transverse wrinkling, on the other hand, is very indistinct.

The specimens agree in all respects with typical specimens of *Pityophyllum longifolium* (NATH.) MÖLLER. This species has been found in Scania, not only at Dompäng, but also at Bjuf, Hälsingborg, Pålsjö and Hoer. It has also been recorded from Bornholm, Turkestan and possibly from other localities.

Summary and Conclusion.

In Tables 1 and 2 the plant-remains described above from Sofiero and Dompäng are enumerated. The occurrence of identical or related species in some important comparable floras has been noted for comparison.

Table 1. **The geographical and geological distribution of the fossil plants from Sofiero.**

	Sofiero	Scania: Bjuf: Lower Rhaetic	Scania: Höganäs (Older): Lower Rhaetic	Scania: Stabbarp: Middle Rhaetic	Scania: Höganäs (Younger): Upper Rhaetic	Scania: Hälsingborg: Upper Rhaetic	Scania: Pålsjö: Uppermost Rhaetic	Scania: Hoer: Lower Liassic	Scania: Dompäng: Lower Liassic	Poland: Rhaetic	Bornholm: Vellengsby: Rhaetic	Bornholm: Bagaa: Liassic	Franconia: Nürnberg: Lower Liassic	Franconia: Other localities: Lower Liassic	Austria: Lower Liassic	Other localities	
1.	*Dictyophyllum Nilssoni* (BRGN.) GÖPP.	—	—	—	—	+	+	+	+	+	+	?	—	+	—		1.
2.	*cf. Andriania baruthina* F. BRAUN	—	—	—	—	—	—	+	—	—	—	—	+	+	—		2.
3.	*Sagenopteris Nilssoniana* (BRGN.) WARD	—	—	—	—	—	+	+	+	—	—	+	—	+	—	Rödalsberg (S. E. Scania)?: Rhaetic.	3.
4.	*Marattiopsis hoerensis* (SCHIMP.) THOMAS	—	—	—	—	—	—	+	—	—	—	—	—	—	—		4.
5.	*Nilssonia polymorpha* SCHENK	+	+	—	—	—	+	+	+	—	+	+	—	+	+		5.
6.	*Anomozamites gracilis* NATH.	+	+	—	—	—	+	+	—	—	—	—	+	—	—		6.
7.	*Ginkgo Hermelini* (NATH.) HARTZ.	—	—	—	—	—	—	—	+	—	—	—	—	—	—	Cape Stewart (East Greenland): Rhaetic.	7.
8.	*Baiera taeniata* F. BRAUN	—	—	+	—	—	—	+	+	—	—	—	+	+	+		8.
9.	» *cf. angustiloba* HEER	—	—	+	—	—	—	+	—	—	—	—	+	—	—	Siberia, Spitzbergen(?) and Transbaikalia(?): Middle Jurassic; China: Jurassic.	9.
10.	» *cf. spectabilis* NATH.	—	—	+	—	—	—	+	—	—	—	—	—	—	—		10.
11.	» *cf. Czekanowskiana* HEER	—	—	—	—	—	—	—	—	—	?	?	—	—	—	Bornholm (Rönne): Rhaetic or Liassic; Siberia: Jurassic.	11.
12.	*Czekanowskia rigida* HEER	+	—	+	—	—	—	+	—	+	+	?	—	—	—	Greenland: Rhaetic; Russia, Siberia and Japan(?): Middle Jurassic; China: Jurassic.	12.
	Number of species common with the fossil flora of Sofiero	3	2	4	0	1	4	10	5	2	3	2	4	5	2		

Table 2. **The geographical and geological distribution of the fossil plants from Dompäng.**

	D o m p ä n g	Scania: Bjuf: Lower Rhaetic	Scania: Höganäs (Older): Lower Rhaetic	Scania: Stabbarp: Middle Rhaetic	Scania: Höganäs (Younger): Upper Rhaetic	Scania: Hälsingborg: Upper Rhaetic	Scania: Pålsjö: Uppermost Rhaetic	Scania: Hoer: Lower Liassic	Scania: Sofiero: Lower Liassic	Poland: Rhaetic	Bornholm: Vellengsby: Rhaetic	Bornholm: Bagaa: Liassic	Franconia: Nürnberg: Lower Liassic	Franconia: Other localities: Lower Liassic	Austria: Lower Liassic	Other localities	
1.	*Equisetites Mobergii* MÖLLER . .	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Kurremölla (S. E. Scania): Middle or Upper Jurassic?.	1.
2.	*cf. Thaumatopteris Schenki* NATH.	—	—	+	+	+	+	+	—	+	+	+	+	+	—		2.
3.	*Dictyophyllum Nilssoni* (BRGN.) GÖPP.	—	—	—	—	+	+	+	+	+	+	?	—	+	—		3.
4.	*Sagenopteris Nilssoniana* (BRGN.) WARD.	—	—	—	—	—	+	+	+	—	—	+	—	+	—	Rödalsberg (S. E. Scania)?: Rhaetic.	4.
5.	*Nilssonia polymorpha* SCHENK. . .	+	+	—	—	—	+	+	+	—	+	+	—	+	+		5.
6.	*Ginkgo Hermelini* (NATH.) HARTZ	—	—	—	—	—	—	—	+	—	—	—	—	—	—	Cap Stewart (East Greenland): Rhaetic.	6.
7.	*Baiera taeniata* F. BRAUN	—	—	+	—	—	—	+	+	—	—	—	+	+	+		7.
8.	*Pityophyllum longifolium* (NATH.) MÖLLER	—	—	—	+	+	+	+	—	—	+	+	—	—	—		8.
	Number of species common with the fossil flora of Dompäng . .	1	1	2	2	3	5	6	5	2	4	4	2	5	2		

Table 1 shows that the flora of Sofiero has a close affinity whith that of Hoer, as described by ANTEVS (1919), no less than 10 species of the total number of 12 making up the Sofiero flora being common to both floras.

Among identical forms, *Dictyophyllum Nilssoni*, *Sagenopteris Nilssoniana*, *Marattiopsis hoerensis* and *Baiera taeniata* are particularly to be noted as belonging to the commonest species. *Marattiopsis hoerensis* has hitherto only been recorded from Hoer and Sofiero. The great similarity of the fossil flora of Sofiero with that of Hoer shows that the geological age of these floras must be very nearly the same and certainly Lower Liassic (compare NATHORST 1910, p. 508 and 519; ANTEVS 1919, p. 60).

The resemblance to the flora of Pålsjö is also very close. The number of identical species is only 4, but it must be borne in mind that the flora of Pålsjö has yielded a much smaller number of species than that of Hoer. A comparison of the Pålsjö flora with those of Sofiero and Hoer gives a striking illustration to the almost imperceptible transition of the Rhaetic flora into that of the Lower Liassic, as found in Scania.

Table 2 shows the correlation of the fossil flora of Dompäng with other more or less contemporaneous floras. The closest resemblance is shown to the floras of Pålsjö, Sofiero and Hoer. Of the 8 species constituting the Dompäng flora, 5 are common with Pålsjö, 6 with Hoer and 5 with Sofiero.

As the Pålsjö flora numbers 26 species (NATHORST 1876), the Hoer flora 51 (ANTEVS 1919) and the Sofiero flora 12, the percentage of common species, if properly expressed, will be found to afford very little evidence for settling the question of an Upper Rhaetic or Lower Liassic age. One of the species of the Dompäng flora, *Equisetites Mobergii*, however, throws some additional light on the question of the geological age. It is characteristic of the Kurremölla flora (MÖLLER & HALLE 1913), which is most probably younger than the flora of Hoer. It seems probable, therefore, that the Dompäng flora is more closely comparable with the floras of Sofiero and Hoer than with that of Pålsjö, or may even be a little younger. NATHORST in his latest summary of the palaeontological horizons in the Rhaetic-Liassic of Scania (NATHORST 1910, p. 520) placed the Dompäng beds somewhat higher than the Hoer sandstone, as equivalent with the so called *Ammonites* bed. The review of the flora given above is not opposed to this interpretation.

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Explanation of Plates.

(All figures are in natural size, if not otherwise stated.)

Plate 1.

Fig. 1. *Equisetites* sp. Impression of one internode with both nodes. (Sofiero).

Figs. 2—5. *Cf. Andriania baruthina* F BRAUN. Fragments of pinnae. Figs. 2—3, impression of the lower side of the pinna; fig. 3, magnification of fig. 2. Figs. 4—5, impression of the upper side of the pinna; fig. 5, magnification of fig. 4. (Sofiero).

Fig. 6. *Cf. Thaumatopteris Schenki* NATH. Impression of the lower side of the pinna. (Dompäng).

Fig. 7. *Sagenopteris Nilssoniana* (BRGN.) WARD. Impression of the upper side of the pinna. (Sofiero).

Figs. 8—9. *Sagenopteris Nilssoniana* (BRGN.) WARD. Fig. 8, impression of the lower side of the pinna; fig. 9, upper side of the pinna. (Dompäng).

Fig. 10. *Sagenopteris Nilssoniana* (BRGN.) WARD. Impressions of three small pinnae, probably belonging to a young leaf of this species. (Sofiero).

Figs. 11—12. *Anomozamites gracilis* NATH. Fig. 11, impression of the middle part of a leaf; fig. 12, the lower part of a leaf. (Sofiero).

Fig. 13. *Ginkgo Hermelini* (NATH.) HARTZ. (Sofiero).

Figs. 14—15. *Ginkgo Hermelini* (NATH.) HARTZ. (Dompäng).

Figs. 16 & 18. *Baiera taeniata* F. BRAUN. (Sofiero).
Fig. 17. » » » (Dompäng).
Fig. 19. *Baiera cf. spectabilis* NATH. (Sofiero).
Fig. 20. *Ginkgo* or *Baiera* sp. (Sofiero).
Fig. 21. *Baiera cf. angustiloba* HEER. (Sofiero).

Plate 2.

Fig. 1. *Dictyophyllum Nilssoni* (BRGN.) GÖPP. (Dompäng).
Figs. 2—3. *Marattiopsis hoerensis* (SCHIMP.) THOMAS. Fig. 2, impression of the middle part of the pinna; fig. 3, impression of the basal part of the pinna, showing the base characteristic of this species. (Sofiero).
Fig. 4. *Nilssonia polymorpha* SCHENK. Impression of the lower side of the leaf. (Sofiero).
Figs. 5—6. *Nilssonia polymorpha* SCHENK. (Dompäng).
Fig. 7. *Ginkgo* or *Baiera* sp. (Sofiero).
Fig. 8. *Baiera cf. Czekanowskiana* HEER. (Sofiero).
Fig. 9. *Czekanowskia rigida* HEER. (Sofiero).
Figs. 10—11. *Pityophyllum longifolium* (NATH.) MÖLLER. (Dompäng).
Fig. 12. *Anomozamites gracilis* NATH. Impression of the middle and lower parts of the leaf, the petiole being clearly shown. (Sofiero).

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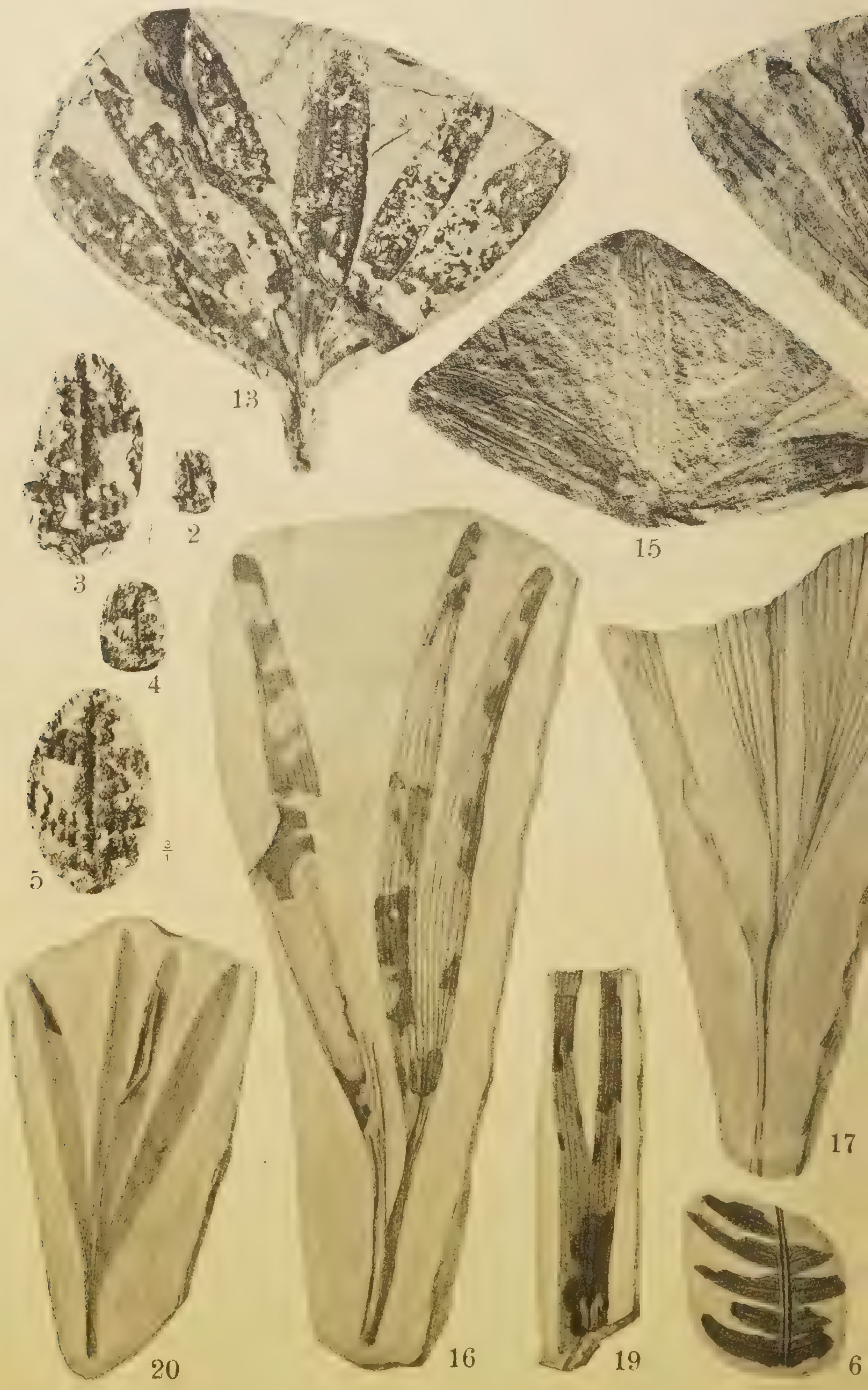

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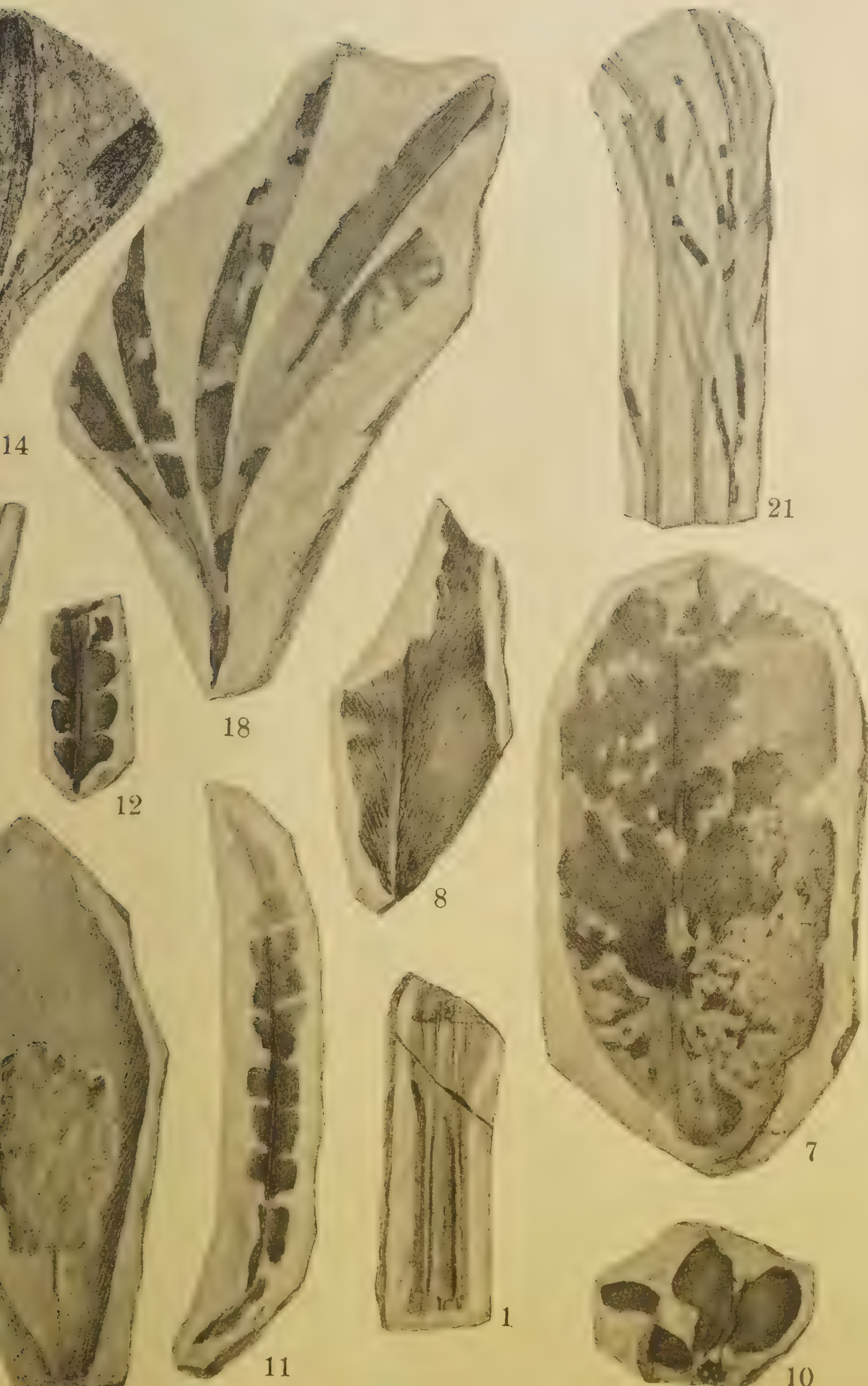

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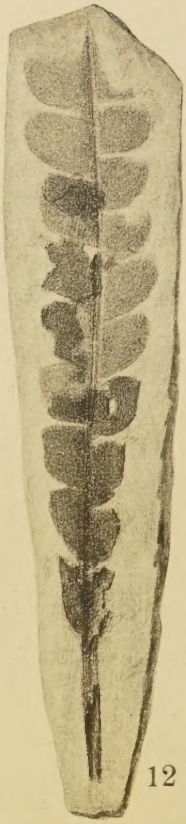

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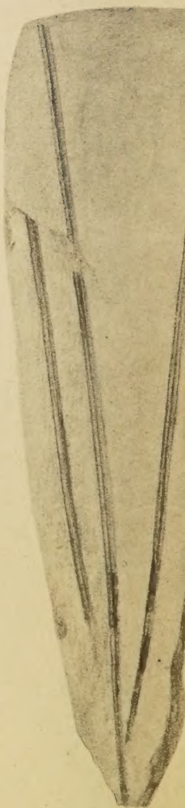

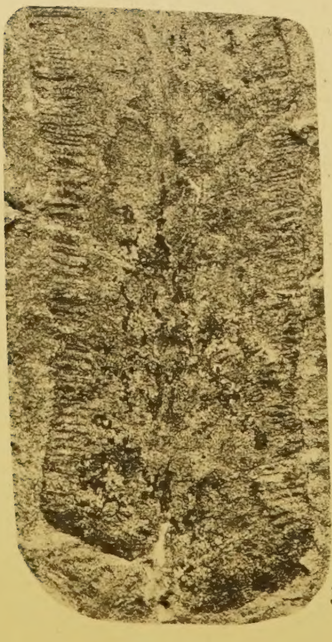

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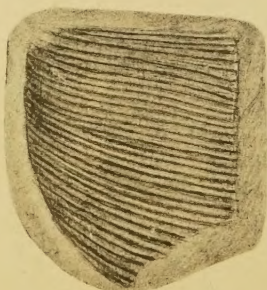

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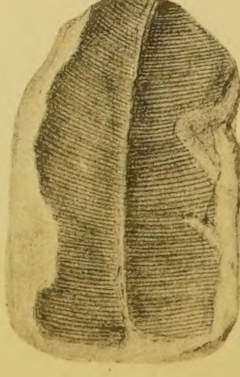

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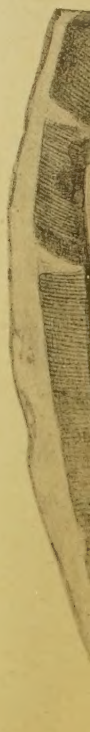

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Pl. 2.


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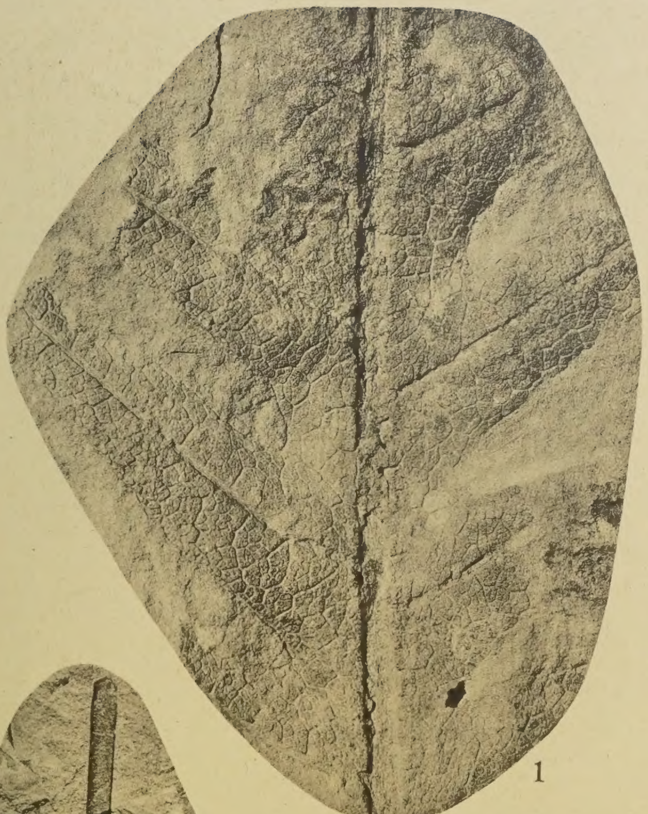
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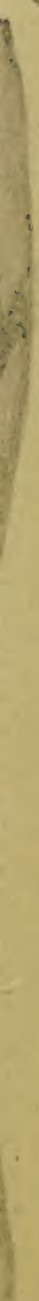
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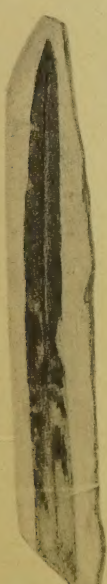
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